The role of introduction pathways on the fate of introduced species

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Ars longa, vita brevis

Hippocrates

Your Excellency may easily judge of my surprise,
on looking round, to behold hedges of aloes
and Indian figs and other proofs of a southern climate,
and to see a great city below me, with towers,
and palaces, and a grand cathedral.

Washington Irving, Tales of the Alhambra

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Si he de definir l'etapa de la tesi amb una paraula, aquesta paraula és "gràcies". Sento una immensa gratitud cap a moltíssimes persones. Cinc anys de tesi són cinc anys de vida, en els que es comparteixen moltes vivències. Així que gràcies a tots vosaltres per ser-hi, per compartir la vida, per recolzar-me, ~~per aguantar-me~~, per estimar-me, i per fer-me sentir estimat. No seria possible sense vosaltres.

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Abstract

Biological invasions are one of the main drivers of global change, with pervasive impacts on biodiversity, ecosystem functioning and the global economy. They start with the transport of organisms beyond their native range, intentionally and/or unintentionally, through introduction pathways. Upon introduction, species vary substantially in their ability to overcome filters to survival, reproduction and dispersal, which can be summarised as their fate. Introduction pathways can also shape the fate of introduced species, as they summarize the initial conditions of introduction and other key features of the introduction process and even some biological attributes of the introduced species. However, few studies have addressed how introduction pathways shape invasion success in combination with other factors, and how they modulate the invaded niche. This lack of insights limits the understanding of the invasion process, and the scope of management actions aiming at preventing invasion. Therefore, the main goal of this thesis is to focus on introduction pathways to deepen our understanding of the mechanisms underlying the fate of introduced species.

Invasion success is an important dimension of the fate of introduced species, assessed in this thesis through a set of proxies, namely range size (geographical spread) and niche breadth (habitat and climate ranges, and degree of habitat specialization), at contrasting spatial and temporal scales. The thesis provides evidence of substantial similarities in range size across species introduced through different pathways and among animals and, our main system study, plants. However, species introduced as contaminants of commodities become more widespread over time than those animals and plants escaping from captivity or cultivation, while those spreading unaided did not become more widespread over time (Chapter 2). Among non-native plants, those introduced unintentionally achieve similar or even greater invasion success than those introduced intentionally (Chapters 2 and 3). Similarly, invasion success in terms of niche breadth is largely unrelated to introduction pathway, independently of how niche breadth was assessed (Chapters 3 and 4). However, plants introduced both intentionally and unintentionally invaded more habitats than those introduced only unintentionally (Chapter 4). Overall, the thesis supports that economic use is not necessary for invasion success (Chapters 2, 3 and 4).

This thesis supports that non-native plants sharing an introduction pathway also tend to share some biological attributes (i.e. a “functional syndrome”), in turn which could modulate pathway-specific differences in invasion success. Thus, compared to intentionally introduced plants, those unintentionally introduced tend to be shorter and to have wider climatic niches in their native range, and are more likely to be epizoochorous and annual herbs. Moreover, plants introduced both intentionally and unintentionally are likely to be herbs and tend to be short with wide native climatic niches and higher residence time (Chapters 3, 4 and 5). Non-native plants with a common pathway can also share features of the introduction process. Our analyses on temporal trends in pathway importance and of pathway-specific differences in the invaded niche, are consistent with the idea that unintentionally introduced plants have diverse introduction epicentres encompassing croplands and urban areas, while intentional introductions could occur mostly in urban areas (Chapters 2, 3 and 4).

Introduction pathways are of secondary importance to explain invasion success when species biological attributes and features of the introduction process are considered. Minimum residence time is often a major driver of range size across animals and plants, and of niche breadth among plants, showing that older introductions tend to be more successful. The breadth of the climatic niche in the native range is positively associated with that in the invaded range, suggesting that pre-adaptation to a wide niche can also shape the fate of introduced species (Chapter 2, 3 and 4).

This thesis also addresses the invaded niche, a second dimension of the fate of introduced species. Animals and plants introduced through different pathways tend to invade slightly different types of environmental conditions, as supported by low overlap among hotspots of invasion across pathways. Anthropogenic disturbance generally increases the number of species introduced through different pathways, although waterbodies are relevant for deliberate release of many fish, while species that spread unaided concentrate near dispersal corridors (Chapter 2). The thesis has also explored pathway-specific differences in niche harshness among non-native plants, showing that the association depends on the type of stress, with dry and saline conditions being mostly invaded by intentionally and unintentionally introduced ones, respectively. The link between pathways and the invasion of high elevations is inconsistent between studies, suggesting context dependency (Chapters 3 and 4). Pathway-specific differences in niche harshness are smaller than those related to habitat type and land-cover. Unintentionally introduced plants tend to be more prevalent in anthropogenic habitats and with increasing cropland land-cover (Chapter 3 and 4).

This thesis provides further insights into the fate of introduced species by comparing the occupied climatic conditions between the native and the invaded range (Chapter 5). Most non-native plants invade similar climatic conditions in both ranges, supporting the niche conservatism hypothesis. Introduction pathways are of secondary importance to species biological attributes and minimum residence time. The main driver of niche conservatism is the breadth of the native climatic niche, followed by minimum residence time and growth form, all of which have positive effects (Chapter 5).

The findings of this thesis support that introduction pathways are associated with the fate of introduced species, but that this association depends on the context and which aspect of invasion is studied. Over time, plants introduced through different pathways largely spread the same in geographical and environmental space (i.e. similar range size and niche breadth). This process of spread is coupled by pathway-specific differences in the invaded niche (i.e. shaped mostly anthropogenic disturbance and elevation), and by low overlap among hotspots of invasion. Moreover, these invasion patterns might largely occur in climatic conditions similar to those already occupied in the native range, a similarity that is largely independent of introduction pathways.

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Chapter 1

General introduction and methods

1.1. General introduction

Biological invasions

The current state of the Biosphere is unprecedented, as human socioeconomic activity has triggered a global wave of biological invasions (W. Dawson et al., 2017; Elton, 1958; Lockwood et al., 2007). For example, a number of plant species equivalent to the native flora of the European continent (ca. 13,000) has established populations outside their native range (Van Kleunen et al., 2015). The consequences of such invasions are pervasive, including biodiversity loss, as non-native species were listed as the cause of 25% of plant extinctions and 33% of animal extinctions in recent years (Blackburn et al., 2019). Negative impacts of biological invasions extend into the global economy, since the mean annual cost of biological invasions for the period 1970-2017 was 20 times higher than the combined budgets of the United Nations and the World Health Organization in the years 2016-2017 (Diagne et al., 2021). As new invasions continue unabated (Seebens et al., 2017), a deeper understanding of biological invasions is a research question of global interest.

Biological invasions are a complex phenomenon, in which the introduction of different species can have very different outcomes. Overall, the invasion process can be summarised into two major steps, in which species vary in their ability to overcome a series of filters (Blackburn et al., 2011). First, introduction pathways overcome a geographic filter by transporting species beyond their native range into an introduced range (Hulme et al., 2008). Second, upon introduction, the fate of introduced species depends on overcoming very diverse filters to survival, reproduction and dispersal; according to the interplay of the species biological attributes, the characteristics of the recipient location, and the features of the introduction process (Catford et al., 2009; Pyšek et al., 2020). This dissertation aims to connect both steps of invasion to bring deeper understanding on the invasion process.

Human-mediated transport of species: introduction pathways and other features of the introduction process

The human-mediated transport of species beyond their native range is the starting point of all biological invasions. The impact of such transport on the fate of introduced species can be studied through the features of the introduction process, which describe how and why species are transported (introduction pathways), when species are introduced (minimum residence time), where they are introduced (introduction epicentres) and in which numbers (propagule and colonization pressure).

Introduction pathways (*sensu* Hulme et al., 2008) are the focus I used in this thesis to advance our understanding of biological invasions. The role of introduction pathways at explaining the fate of introduced species is poorly known: only one fourth of macroecological studies of invasion patterns in a recent survey considered socio-economic factors (which include pathways; 27 out of 102 studies; Pyšek et al., 2020). Introduction pathways conceptualize the diversity of processes responsible for the transport and introduction of non-native species (Harrower et al., 2018; Hulme et al., 2008; Kowarik & von der Lippe, 2007). The widely used pathway classification of Hulme et al. (2008) assigns pathways into six main categories:

1. **Release**: intentional introduction of species to the environment, to provide some service to humans. Examples include biological control, the use of plants for erosion control, or stocking with fish, birds and mammals for hunting.
2. **Escape**: intentional introduction of species to be kept in captivity or cultivation, which subsequently escape. Examples include pet ownership (e.g. terraria, aquaria), zoos, or the cultivation of plants (e.g. agriculture, forestry, gardening).
3. **Contaminant**: unintentional introduction of species that are ecologically related to a traded commodity. Examples include the trade of plants or animals carrying pests and parasites, or the sowing of seeds containing agricultural weeds.
4. **Stowaway**: unintentional introduction of species attached to a transport vessel or associated equipment. Examples include species hitchhiking in/on a vessel (plane, ship, car…), or in/on what is being transported (commodities, containers, luggage…), or on who is being transported (tourist's clothing…).
5. **Corridor**: dispersal of species following the construction of transport infrastructures in whose absence spread would not have been possible. Examples include marine taxa dispersing from the Red Sea to the Mediterranean Sea.
6. **Unaided**: dispersal of species on their own means, following their introduction through any of the previous pathways. Examples include migrant birds.

Overall, species may often be introduced through more than one pathway, as found in plants with multiple human economic uses (van Kleunen et al., 2020), or associated with specific commodities and to unspecific vectors (Buttenschøn et al., 2009); or they can have a complex invasion history encompassing both intentional and unintentional introduction (Sanz-Elorza et al., 2004a).

A main feature of the introduction process is propagule pressure, which is the number of propagules (adults, seeds or vegetative fragments) introduced to an area (Lockwood et al., 2005). An elevated propagule pressure reduces the effect of demographic and environmental stochasticity on non-native populations, and thus makes population extinction less likely (Lockwood et al., 2005; van Kleunen, Bossdorf, et al., 2018). Propagule pressure is very difficult to quantify at large spatial extents (Pyšek et al., 2020), and suitable proxies vary across taxonomic groups. For intentionally introduced plants, these proxies include availability or sales in nurseries, and frequency of cultivation in gardens, generally showing positive correlations to population establishment and spread (Kinlock et al., 2022; Maurel et al., 2016). However, quantitative data is less available for unintentional pathways, which are also very heterogeneous (Harrower et al., 2018; Kowarik & von der Lippe, 2007; Richardson & Pyšek, 2012). A related concept, closely related to the richness of non-native taxa, is colonization pressure (i.e. the number of species introduced to an area), which would be highest in areas with high socio-economic activity (Blackburn et al., 2020; Lockwood et al., 2009).

In relation to the temporal aspect of introduction, the most accepted proxy has become minimum residence time, which is a conservative metric of how long a species has been in the wild in a recipient territory (Rejmánek, 2000). Minimum residence time generally correlates positively to geographical spread (Fristoe et al., 2021; Gassó et al., 2009), the number of invaded habitats (Lazzaro et al., 2020) and climatic niche breadth (Banerjee et al., 2021). The importance of minimum residence time probably relies on its role as a proxy of other variables (i.e. time is not causal per se), such as propagule pressure, the number of generations (in interaction with species life span), the number of opportunities to establish, disperse, and evolve local adaptation and adaptive phenotypic plasticity (Lockwood et al., 2007; Pyšek et al., 2020). Residence time can also shed light on the transformation of introduction pathways over time, since changes in human society transform the motivations and the processes behind the introduction of species (Mack & Lonsdale, 2001; Sanz-Elorza, Mateo, et al., 2009; Seebens et al., 2022).

Finally, the spatial component of the introduction process can be proxied by introduction epicentres, which are the sites of initial introduction (i.e. where propagule pressure is exerted on the surrounding environment; Early et al., 2016). They are mostly areas with some specific socio-economic activity, such as urban areas, trade and transport infrastructures or agricultural fields (Conn, 2012; Cossu et al., 2020; Lucardi et al., 2020). Since different types of socio-economic activity are associated with different introduction pathways, previous research in plants suggests that species introduced through the same pathway tend to share introduction epicentres (Ni & Hulme, 2021; Padayachee et al., 2017). Although this has implications for the type of environmental conditions immediately available for colonization (Donaldson et al., 2014; Ni & Hulme, 2021), many gaps remain in the knowledge of how introduction pathways shape the type of invaded environmental conditions (Donaldson et al., 2014; González-Moreno et al., 2013).

The fate of introduced species

A long-standing goal of invasion ecology is to predict the fate of non-native species once introduced to a recipient area (i.e. to establish patterns and processes in the outcome of their introduction). Many studies have approached the fate of introduced species through the lens of "invasion success", i.e. any measurement of a species' ability to overcome filters to survival, reproduction and dispersal (Carboni et al., 2016; Catford et al., 2016; Fristoe et al., 2021; Giulio et al., 2020; Palma et al., 2021; van Kleunen, Bossdorf, et al., 2018). In this thesis I have quantified invasion success through two complementary metrics: range size (i.e. geographical spread), and the less-studied niche breadth (i.e. range of invaded environmental conditions; Catford et al., 2016). By linking invasion success to species' introduction pathway and attributes, we can bring insights to prioritize management of pathways and species associated with higher success (McGeoch et al., 2016). Invasion success can also be measured categorically, by classifying a species along an introduction-naturalization-invasion continuum, according to their ability to form persistent populations and spread (Blackburn et al., 2011). In this thesis I have opted to work with continuous metrics of invasion success, since no continuous metric clearly separates invasive from non-invasive species (Catford et al., 2016).

Besides invasion success, the fate of introduced species can be approximated by niche properties. An example is niche harshness, which indicates the invasion of stressful areas that jeopardize plant survival, reproduction and dispersal (Alpert et al., 2000; Zefferman et al., 2015). This dimension of the fate of introduced species can also yield insights into which environmental conditions are most susceptible to invasion (McGeoch et al., 2016). Furthermore, from a climatic standpoint, different non-native species are placed in a gradient of niche conservatism, depending on how similar are the occupied climatic conditions between the native and the invaded ranges (Atwater et al., 2018; Liu et al., 2020). Such contraction or broadening of the conditions in which the species is able to maintain fitness has implications for the reliability of climate matching to predict non-native species' spread (Liu et al., 2022).

The interplay of multiple factors shapes the fate of introduced species

As commented, upon being transported by introduction pathways, the fate of non-native species will vary depending on their ability to overcome filters to survival, reproduction and dispersal. In more general terms, the distribution of species has been conceptualized through the interplay of abiotic conditions, biotic interactions and dispersal limitations (Franklin, 2010; Gaston, 2003; Pulliam, 2000; Soberón & Peterson, 2005). In line with this notion, recent conceptual frameworks outline a three-way classification of factors that shape invasions (Pyšek et al., 2020): species biological attributes, characteristics of the recipient location, and features of the introduction process (discussed above).

Species biological attributes are defined in this thesis as any measurable variables at the individual, population or species level, that relate to plant fitness (survival, reproduction and dispersal). This broad definition of attributes encompasses traits, commonly defined as morphological, physiological or phenological characteristics measured at the individual level, without reference to the environment (S. K. Dawson et al., 2021; Violle et al., 2007).

Among the whole suite of potential attributes, this thesis focuses on five attributes relevant for plant ecology, and that influence the fate of introduced plants (Gassó et al., 2009; Pyšek & Richardson, 2007; Wilson et al., 2007). (1) Plant growth form combines longevity and woodiness, summarises life-history trade-offs and functional attributes such as leaf and root traits (Poppenwimer et al., 2023), and has been linked to variation in invasion success (Ainsworth & Drake, 2020; Razanajatovo et al., 2016). (2) Plant height informs on competition for light and seed dispersal distance (Thomson et al., 2011), and sometimes correlates positively to greater spread and population establishment (Kinlock et al., 2022; Speek et al., 2011). Reproductive traits can also shape the fate of introduced species. (3) Dispersal syndrome reflects how seeds travel away from the parental individuals (Fenner & Thompson, 2005), which can influence a plant's ability to spread (Gassó et al., 2009; Wilson et al., 2007). Non-sexual modes of reproduction can also influence a species fate, since (4) vegetative reproduction can produce clones that colonize efficiently (Lloret et al., 2005). Furthermore, the (5) breadth of the niche in the native range is an attribute that emerges from the interplay of physiological tolerances, biotic interactions and dispersal limitations (see below), and that is generally positively correlated to invasion success (Bucharova & van Kleunen, 2009; Gallagher et al., 2015; Kühn et al., 2004; Vázquez, 2006).

On the other hand, multiple characteristics of the recipient location can influence the fate of introduced species, including disturbance, abiotic conditions, and the biotic community (Pyšek et al., 2010, 2020). Disturbance (biomass removal and/or alteration of abiotic conditions) may make recipient locations more vulnerable to invasion by increasing the available resources and generating suitable habitats (Davis et al., 2000; Jauni et al., 2015). Many studies have reported a positive effect of disturbance on the presence and richness of non-native plants, using common proxies related to human socio-economic activity (Chytrý et al., 2008; Gassó et al., 2012; González-Moreno et al., 2014; Jauni et al., 2015; Wagner et al., 2021). These empirical observations probably relate to the high incidence among non-native plants of early-successional attributes, such as fast growth and acquisitive resource strategies (Martin et al., 2009).

Abiotic conditions shape the fate of introduced species by filtering their distribution according to each species Hutchinsonian niche: the set of environmental conditions which sustain populations (Pulliam, 2000). Following the niche conservatism hypothesis, a non-native species' fitness will be highest in recipient locations with environmental conditions that match their native range, which is the conceptual underpinning of models that use climate matching to predict species' spread (Haeuser et al., 2018; Hayes & Barry, 2008; McGregor et al., 2012). However, following unclear mechanisms, some species can invade climatic conditions that differ substantially from those in their native range (i.e. niche shifts;(Atwater et al., 2018; Early & Sax, 2014; Petitpierre et al., 2012).

The result of the filtering exerted by abiotic conditions is often an accumulation of non-native plants in areas with mild climates (e.g. abundant rainfall and infrequent frost), low levels of stress (e.g. salinity), and abundant nutrients (Alexander et al., 2016; Alpert et al., 2000; W. Dawson et al., 2017; González-Moreno et al., 2014; Pino et al., 2005; Zefferman et al., 2015). In some circumstances, the invasion of harsh environmental conditions is aided by disturbance (Alexander et al., 2016; Alpert et al., 2000; Zefferman et al., 2015). Another key abiotic driver of invasion is elevation, the general pattern being that lowlands are more invaded than high elevation areas (Alexander et al., 2011, 2016). Elevation is often considered a proxy of previously described drivers: climates are more mild and terrain more accessible in lower elevations, facilitating socio-economic activity and disturbance (Alexander et al., 2016; Clotet et al., 2016; Gassó et al., 2009). Similarly to abiotic conditions, the recipient biotic community will also exert environmental filtering (Carboni et al., 2016; Divíšek et al., 2018; Traveset & Richardson, 2014), which lies outside the scope of this thesis.

1.2. Objectives

The fate of introduced species is the outcome of a complex set of factors, both intrinsic and external (environmental and human-mediated) that affect the introduction process and the further fate of introduced species. In this thesis, I seek to advance our understanding of biological invasions by testing the effect of introduction pathways on different dimensions of the fate of introduced species, from a macroecological perspective (Fig. 1.1).

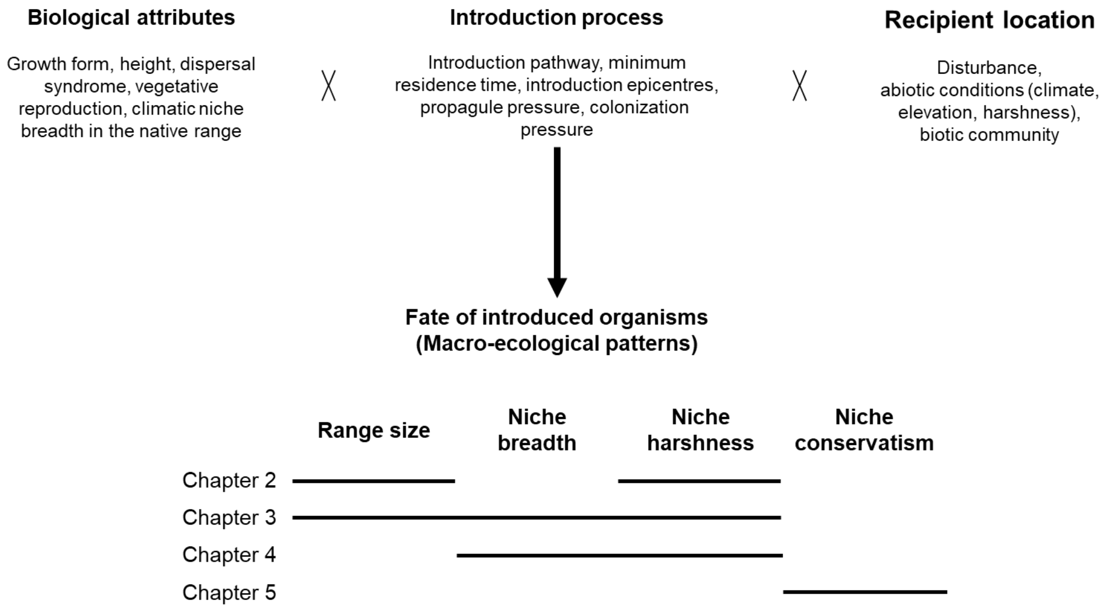

Fig. 1.1. Conceptual diagram of factors affecting the fate of introduced species.

To achieve this objective, we addressed the following research questions:

- Q1. Do introduction pathways determine similar invasion success (i.e. range size) on contrasting species groups?
- Q2. Do biological attributes and history modulate pathway effects on plant species success in space and time?
- Q3. Do pathways affect invaded niche conditions in terms of breadth and harshness?
- Q4. Do pathways modulate niche conservatism between native and recipient areas?

Questions are addressed in different chapters. Chapter 2 explores how introduction pathways shape invasion success in conjunction with minimum residence time across animals and plants. Furthermore, it assesses the spatial pattern and underlying environmental drivers of the accumulation of non-native animals and plants in richness hotspots. Chapter 3 tests how invasion success, in terms of range size and niche breadth, is shaped by introduction pathways in combination and interaction with selected species biological attributes and minimum residence time. Moreover, it explores long-term temporal trends in the contribution of pathways to a non-native flora. It finally tests for pathway-specific differences in the type of invaded conditions (i.e. invaded niche).

Chapter 4 examines whether introduction pathways shape the invaded niche, in terms of niche breadth (i.e. invasion success) and niche harshness. In both cases, it accounts for other variables, such as species' biological attributes and minimum residence time shaping invasion success, and for habitat and land-cover variables shaping niche harshness. Finally, Chapter 5 addresses the niche conservatism hypothesis, relating the type of invaded climatic conditions in the native and invaded ranges to introduction pathways, species biological attributes and minimum residence time.

1.3. General methods

This thesis relied on the pathway classification of Hulme et al. (2008), which has become a global standard (Wilson et al., 2020). Such classification encompasses six main categories, which were adapted in each chapter according to the research question and the sample size (Table 1.1). Pathway data was gathered from expert consultation and literature review following international guidelines (Harrower et al., 2018), building on the information gathered by the EXOCAT database (Andreu & Pino, 2013; Rotchés-Ribalta et al., 2021), and the checklist of the non-native Catalan flora (Aymerich & Sáez, 2019a).

The fate of introduced species was addressed through the analysis of macroecological patterns (Pyšek et al., 2020), gathered from large databases containing georeferenced occurrences in the invaded range, and data on invaded environmental conditions (Table 1). These were combined with climatic and land-cover databases to further characterize the invaded niche. References are provided in each chapter as appropriate.

Table 1.1. Overview of the chapters of this thesis.

	Chapter 2	Chapter 3	Chapter 4	Chapter 5
Species group	Plants and animals	Plants	Plants	Plants
Species number	869	1046 (temporal trends) + 77 (invasion success & invaded niche)	220	164
Pathway categories	Release, escape, contaminant, stowaway, unaided	Agriculture/Forestry, gardening, unintentionally	Both intentional & unintentional, only intentional, only unintentional	Agriculture, forestry, gardening, unintentional
Residence time	1762 – 2019	Before 1500 – 2019	1550 – 2021	1762 – 2021
Extent	Catalonia (NE Spain)	Barcelona province & Catalonia	Europe	Spain (mainland) & Global
Specific databases	EXOCAT (Andreu & Pino, 2013; Rotchés-Ribalta et al., 2021)	Aymerich & Sáez (2019a); Clotet et al. (2016)	European Vegetation Archive (EVA; Chytrý et al., 2016)	GBiF (https://www.gbif.org/)

The research questions faced the methodological challenge of accounting for correlated data, either from a phylogenetic or a spatial perspective (Sol et al., 2008). We took multiple approaches to account for phylogenetic relatedness, each tailored to the statistical model needed to answer our research questions: phylogenetic generalized least squares (Symonds & Blomberg, 2014), mixed-effects models (Harrison et al., 2018), or phylogenetic covariates (Diniz-Filho et al., 1998). We accounted for spatial non-independence by including coordinates in models and checking for autocorrelation in residuals (Fletcher & Fortin, 2018).

Chapter 2

Impact of introduction pathways on the spread and geographical distribution of alien species: Implications for preventive management in mediterranean ecosystems

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2.1. Abstract

Aim: To test whether alien species with contrasting introduction pathways differ in range size, geographical distribution and their relationship with environmental variables.

Location: Catalonia (NE Spain).

Methods: We obtained records of 869 alien species from the Catalan alien species database at the 10-km UTM cell scale. For each species, we assigned its introduction pathways and minimum residence time (MRT). We then analysed species' range sizes in relation to their pathways and taxonomic group while accounting for MRT through linear models. We identified hotspots of alien species richness across pathways through local Gi* statistics, and we analysed their spatial congruence. We assessed the environmental drivers of alien species richness across pathways, by means of ordination methods.

Results: Range size was mostly equivalent among pathways, with species that escape or spread unaided reaching smaller range size than species introduced with contaminated commodities. Among taxonomic groups, range was smaller for terrestrial invertebrates compared to plants. The spatial pattern of hotspots of alien species richness showed low congruence across pathways. Proxies that pool the effect of colonization and propagule pressure were the main drivers increasing alien species richness across pathways (except for the unaided pathway).

Main conclusions: Differences among pathways can be related to a lack of human aid (unaided and contaminant pathways) and to trait selection (escape and contaminant pathways), while differences among taxonomic groups (terrestrial invertebrates and plants) may be related to dispersal capacity. The remaining pathways and taxonomic groups were similar in range size, suggesting shared underlying factors. Invasion risk from different human socio-economic activities is spread over our study area rather than concentrated in unique high-risk areas This can be the foundation for a prevention scheme that monitors areas susceptible to invasion for the different pathways.

2.2. Introduction

Biological invasions are one of the main drivers of global change, being responsible for impacts on native species, ecosystem function and considerable economic losses (Pimentel et al., 2005; Vilà et al., 2010, 2011). The Convention on Biological Diversity (CBD) sets the goal of prioritizing invasive species and their introduction pathways (i.e. the processes that result in the introduction of a species from one location to another; Convention on Biological Diversity, 2011; Hulme et al., 2008). To facilitate data exchange across countries and the identification of best management responses, the CBD proposed a classification of pathways which has been widely accepted (Convention on Biological Diversity, 2011; Harrower et al., 2018; Hulme et al., 2008).

Management of biological invasions is mostly focussed on prioritizing species with the highest risk of negative impact on native species, ecosystem functioning or the economy. Nevertheless, this approach can be limited due to insufficient data, for example on unintentional introductions or elusive species. Therefore, it must be balanced with a focus on introduction pathways, prioritized according to the number of introduced species through each pathway and the impact of these species (Essl et al., 2015; McGeoch et al., 2016). Pathway-based management aims at reducing propagule pressure (i.e. the number of introduced individuals and events of introduction of alien species; Lockwood et al., 2005) on the receiving territories.

Previous studies have highlighted the role of pathways in shaping biological invasions, thus supporting the importance of pathway management (Wilson et al., 2009). For example, intentionally introduced plants are more likely to become naturalized than those unintentionally introduced (W. Guo et al., 2019; Pyšek et al., 2011). Moreover, species with multiple introduction pathways increase their probability of causing negative impact (Pergl et al., 2017).

Furthermore, effective management of biological invasions needs to take into account the taxonomic, temporal and spatial variation of pathways, which remain largely unexplored (Essl et al., 2015). For example, alien plants and vertebrates are generally introduced intentionally, while invertebrates are mostly introduced unintentionally (Saul et al., 2017). Moreover, the contribution of the different pathways to the pool of alien species might vary over time (Faulkner et al., 2016; Pyšek et al., 2011). To our knowledge, whether pathways mediate differences in range size (i.e. geographical spread) has only been tested for plants (W. Guo et al., 2019; Pyšek et al., 2011, 2015). Furthermore, how the spatial pattern of alien species richness varies across pathways has not been deeply explored (Essl et al., 2015). Some works suggest differences between unintentionally and intentionally introduced species (Padayachee et al., 2017; Pyšek et al., 2011), and that the relative contribution of different pathways to the alien species pool varies among countries (Essl et al., 2015; Nunes et al., 2015; Turbelin et al., 2017).

The uneven distribution of alien species across territories mirrors the uneven distribution of human population and socio-economic activity (Pyšek et al., 2010). Therefore, a need arises for site-based prioritization in the response to biological invasions, singling out locations that are susceptible (sites at high risk of invasion) and/or sensitive (sites of high conservation value) to invasion (McGeoch et al., 2016). The focus has been put on the spatial patterns of these susceptible sites or invasion hotspots (W. Dawson et al., 2017; Gassó et al., 2009; Pino et al., 2005). These previous studies have highlighted the key role of variables reflecting both colonization (the number of species introduced or released in an area) and propagule pressure (Lockwood et al., 2009). In contrast, the spatial pattern of introduction pathways and their main drivers remains largely undetected, despite some recent works suggesting that cities concentrate intentional introductions (Padayachee et al., 2017), while alien plants introduced unintentionally occur in a wider range of semi-natural habitats (Pyšek et al., 2011).

The present paper uses the CBD pathway classification to assess the usefulness of introduction pathways to explain the spread and geographical distribution of alien species and their main drivers, thus linking introduction pathways and invaded sites (two of the foci for comprehensive prioritization suggested by McGeoch et al. (2016). Specifically, we aim to understand how range size of alien species varies in relation to the different pathways, while checking how this effect is modulated by taxonomic groups, and whether hotspots and drivers of alien species richness are consistent across pathways. To our knowledge, the CBD pathway classification has never been applied to test differences in range size across pathways using data on multiple taxonomic groups.

We hypothesized (H1) that alien species introduced through different pathways would achieve different range sizes as suggested by previous works (W. Guo et al., 2019; Pyšek et al., 2011, 2015). We also hypothesized (H2) that hotspots of richness of alien species would be more spatially congruent through intentional pathways than for unintentional ones, in line with the predominance in cities of intentional introductions across taxonomic groups (Padayachee et al., 2017). We finally hypothesized (H3) that the key role of proxies of colonization and propagule pressure driving the spatial pattern of alien species richness is also observed in that of introduction pathways.

Following the prioritization framework of McGeoch et al. (2016), results will contribute to the prioritization of pathways (priority pathways leading to greater range size) and the joint prioritization of pathways and sites (hotspots of alien species richness across pathways are sites at highest risk of invasion from different human activities).

2.3. Methods

Study area

Catalonia (NE Spain) is a region of 32,000 km^2 located on the Mediterranean coast and bounded on the north by the Pyrenees (Fig. 2.1). The geographical situation (receiving Atlantic, Mediterranean and even Saharan influences), combined with its complex topography (with elevations in the range of 0–3,350 m a.s.l.) leads to sharp climatic gradients. Temperature increases and rainfall decreases towards the south. A continental gradient is present from the coast, with moist and temperate climates, to inland, with drier conditions (Ninyerola et al., 2000). Most favourable areas for human settlement, especially plains and lowlands, display an opposite trend of increasing crop intensification and urbanization (Bielsa et al., 2005; Ibàñez & Buriel, 2010). Human settlement is strongest on the coastal strip, especially around the city of Barcelona (Ibàñez et al., 2002). Industry and trading activities, both currently and in the last century, are particularly concentrated along the coast and in the eastern half of our study area (Pino et al., 2005). Watersheds are characterized by a medium conservation status, with many alterations of human origin including canalizations and reservoirs, built on account of Catalonia's seasonal rainfall pattern (Catalan Water Agency, 2005).

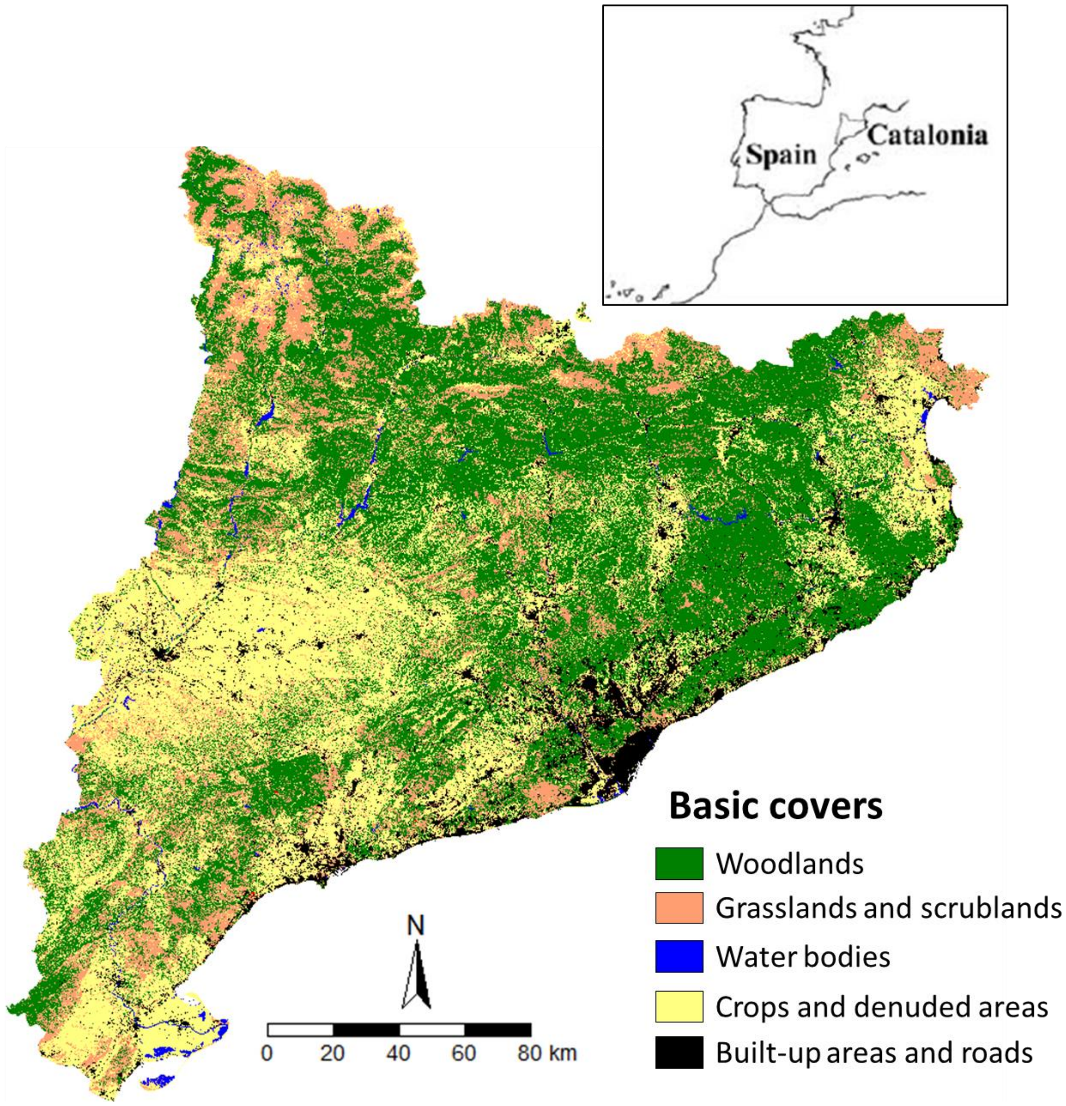


Fig. 2.1. Basic land-cover map of the study area, generalized from the land-cover map of Catalonia (http://www.creaf.uab.cat/mcsc/).

Data collection and preparation

We extracted our data from EXOCAT (http://exocatdb.creaf.cat/base_dades/), a public database that compiles spatially and temporally explicit records of alien species in Catalonia from multiple sources (scientific publications, grey literature, contributions by naturalists, biodiversity managers and citizen scientists). Due to its spatial coverage and recurrent updates, it provides information on the geographical distribution of alien species as well as their origin and introduction pathways, accounting for over 30,000 records of alien species in terrestrial, marine and freshwater ecosystems. We also gathered additional unpublished records (Roura-Pascual et al., 2009).

We selected data from terrestrial and freshwater (hereafter referred as aquatic) taxa introduced after 1500, as there are many information gaps regarding those species introduced earlier (Chytrý et al., 2009; Girado-Beltrán et al., 2015). This yielded a selection of 869 species, most of them belonging to plants (63%), terrestrial vertebrates (18%) and terrestrial invertebrates (11%). We then built a dataset with the following information for each selected alien species (see definitions and calculation details below): (a) range size, (b) taxonomic group, (c) the introduction pathway and (d) minimum residence time (MRT).

Range size corresponded to the number of occupied 10-km UTM cells of each species (N = 381 cells), extracted from EXOCAT. Before its calculation, all geographical data (coordinates, waterbodies, 1-km UTM) were summarized into 10-km UTM cells (i.e. the minimum resolution of EXOCAT data) using database tools. Working at a finer resolution would have implied discarding a sizeable proportion of all records, since the finest resolution available in most literature is the 10-km UTM cell.

Taxonomic group was obtained from EXOCAT and the literature (aquatic status for plants was taken from (Sanz-Elorza et al., 2004a). This resulted in nine taxonomic groups, which were very uneven in sample size. To get a big enough sample size to ensure robustness in statistical tests, we pooled all species into five taxonomic groups of higher level: (a) plants (only vascular plants; both aquatic, N = 27 species; and terrestrial, N = 520), (b) aquatic invertebrates (N = 22), (c) aquatic vertebrates (both fish, N = 34; and amphibians, N = 9), (d) terrestrial invertebrates (N = 100) and (e) terrestrial vertebrates (both reptiles, N = 28; birds, N = 121; and mammals, N = 8). The original nine taxonomic groups were kept for supplementary analyses.

Species' introduction pathways were obtained by reclassifying the EXOCAT pathways into the CBD pathway classification (Convention on Biological Diversity, 2014; Hulme et al., 2008). This reclassification was supported by literature review (Harrower et al., 2018; see Table S1.1). The CBD pathway classification outlines six categories of introduction pathways, differentiated by decreasing human intentionality in the introduction of the species: (a) release (alien species are traded to be deliberately released in nature); (b) escape (alien species are traded to be kept in managed conditions, but they escape or are irresponsibly released from confinement); (c) contaminant (alien species are introduced unknowingly with a commodity they are ecologically associated with); (d) stowaway (unintentional introduction related to human transport, and not linked to a specific commodity); (e) corridor (introduction of aliens possible due to anthropogenic corridors); and (f) unaided (natural dispersal from a donor region where alien species have been introduced through other pathways). Following Harrower et al. (2018), we considered release and escape as intentional pathways, and the others as unintentional, since the escape pathway included the irresponsible release of pets. Additionally, we considered pathways as either unaided (corridor and unaided pathway) or aided (all other pathway categories), according to whether they benefit from propagule and colonization pressure in our study area (aided pathways), or only benefit from these pressures in the area of introduction from which they spread (unaided pathways). In the case of multiple pathways, we selected through literature review those (up to two) that contributed the most to the establishment of a given species. No species could be linked to the corridor pathway, so only the remaining five pathways were analysed in this study.

MRT was the number of years since the species first record in nature (Rejmánek, 2000), included in our analyses since it is known to strongly affect species range size (e.g. for plants in: (assó et al., 2009, 2010; Girado-Beltrán et al., 2015). We calculated MRT as the difference between 2019 and the year of first known record in our study area (Table S1.1 for information sources). We noted that the earliest reliable floristic or faunal records in our study area date from the mid-1700s (similarly to other European datasets; Williamson et al., 2009). Therefore, while we selected species introduced after 1,500, the highest MRT in our study area is 257 (rather than 500).

We also noted that pathways might exhibit temporal dynamics, since the type and relevance of human activities that introduced species have shifted over time (Wilson et al., 2009). Nevertheless, we think that these temporal dynamics do not introduce a significant bias in our results, due to our use of very broad and general pathway categories.

We also calculated pathway-specific alien species richness (i.e. the number of alien species introduced per pathway and 10-km UTM cell). Additionally, we calculated total alien species richness as the total number of alien species in each 10-km UTM cell, with all pathways pooled together. On account of the positive relationship between total alien species richness and area, we calculated these values using only 10-km UTM cells with more than 40% of their surface on our study area, because there was no positive relation between pathway-specific alien species richness and area in the remaining cells (N = 327 cells). Thus, we had five values of pathway-specific alien species richness (one for each pathway) and one value of total alien species richness for each 10-km UTM cell.

We finally selected a set of environmental variables that have been linked to alien species richness in Catalonia and Spain (Table 2.1) based on previous studies, at 10-km UTM scale (Gassó et al., 2009; Girado-Beltrán et al., 2015; Pino et al., 2005). We included proxies of propagule and colonization pressure (urban cover, population density, distance to roads), which are key factors in determining variation in alien species richness across sites (Blackburn et al., 2020; Lockwood et al., 2009). It was not possible to separate the relative contributions of colonization and propagule pressure to pathway-specific alien species richness, since both are positively related and adequate specific proxies remain uncertain (Blackburn et al., 2020; Lockwood et al., 2009). Therefore, we included proxies that pooled both processes in the data analysis and discussed colonization and propagule pressure as a single process behind the pattern of pathway-specific alien species richness. We also note that such proxies do not allow to distinguish between a single introduction event and repeated stocking. Furthermore, our proxies might be insufficient to fully model the introduction of alien species outside of urban areas. We included geographical coordinates as environmental variables, to account for spatial structure and to account for a longitudinal gradient of industry and trade activity (concentrated in eastern parts, both currently and historically; Pino et al., 2005).

Table 2.1. Environmental variables related to pathway-specific species richness with their data sources.

Variable (Abbreviation)	Units	Data source
Climatic		Digital Climatic Atlas of Catalonia, http://www.opengis.uab.cat/acdc/en_index.htm
Mean temperature (TEMP)*	ºC	
Mean rainfall (RAINFALL)	mm	
Topographic		
Mean altitude (ALTITUDE)	m	Cartographical Institute of Catalonia (ICC), http://www.icc.cat/eng/Home-CCCC/Geoinformacio-oficial-PCC/Grup-II-1.-Elevacions
Mean distance to the coastline (DISTCOAST)	m	Land-cover Maps of Catalonia, CREAF, http://www.creaf.uab.es/mcsc/usa/index.htm
Mean distance to main water bodies (DISTWATER)	m	Catalan Water Agency (ACA), http://aca.gencat.cat/ca/laigua/consulta-de-dades/
Landscape		Land-cover Maps of Catalonia, CREAF, http://www.creaf.uab.es/mcsc/usa/index.htm
Cropland cover (CROPCOVER)	%	
Proxies that pool the effects of propagule and colonization pressure		
Built-up cover (URBANCOVER)	%	Land-cover Maps of Catalonia, CREAF, http://www.creaf.uab.es/mcsc/usa/index.htm
Mean distance to roads and railroads (DISTROAD)	m	Catalan Ministry of the Environment (DTES), http://territori.gencat.cat/ca/01_departament/12_cartografia_i_toponimia/
Population density (POPDENS) (2016 census)	hab/km^2	Statistical Institute of Catalonia (IDESCAT), https://biblio.idescat.cat/publicacions/Record/21104
Geographical position		
UTM X coordinate (UTMX)	m	
UTM Y coordinate (UTMY)*	m	

* Indicates variables removed from the pool to control multicollinearity.

Data analyses

To test how the introduction pathway and taxonomic group affected species range size, we performed two separate analyses of covariance (ANCOVA), using the MRT as a continuous covariate (interacting with either pathway or taxonomic group). The effect of the three explanatory variables could not be assessed in a single ANCOVA model due to insufficient sample size in many pathway × group combinations (Table 2.2, Fig. S1.1). We also performed ANCOVA with the original nine taxonomic groups, and three alternative groupings: animals versus. plants, terrestrial versus. aquatic aliens, vertebrates versus. invertebrates (restricting the test to animals). We chose the ANCOVA model since it allowed us to account for the effect of MRT on range size. We declared all explanatory variables as fixed. Range size was ln-transformed for analysis. We assessed pairwise differences in range size among pathways (and taxonomic groups) through post hoc Tukey contrasts of slopes (rate of increase in range size over time). This allowed to establish groups of non-overlapping slopes, which we then used to assess the potential overlap in range size among unintentional and intentional pathways, and among aided and unaided pathways.

To quantify the association between introduction pathway and group based on differences in species frequencies across both classifications, we gathered counts of alien species across all pathway × group combinations into a two-way contingency table (Table 2.2). Similarly, we built two-way contingency tables of counts of alien species across introduction pathways and the original nine taxonomic groups (as well as alternative groupings). Analysis of the contingency tables (through generalized linear models, Poisson errors, log link function) showed statistically significant association regardless of its importance, possibly due to high replication. Following Iannone et al. (2016), we opted to report Cramér's V, which approximates the effect size of the association. Cramér's V ranges from 0 to 1 and indicates weak (<0.3), medium (0.3–0.7) or strong (>0.7) association (Signorell et al., 2020).

To assess the spatial patterns of the pathway-specific and the total alien species richness, we identified hotspots through the local Getis-Ord (Gi*) statistic. The Gi* statistic compares the value of a variable in a specific location and its neighbourhood, to the global mean of that variable across a study region, to identify locations with values significantly different to those expected at random (Getis & Ord, 1992). We established a maximum of 8 neighbours for each 10-km UTM cell. The Gi* statistic can be standardized to produce a Z-score, that can be compared to a standard normal distribution to check for significance (Ord & Getis, 1995). Following Ward et al. (2019), we performed a Bonferroni correction, due to the calculation of a large number of Z-scores (one for each of the 327 10-km UTM cells). Thus, we identified hotspots as those 10-km UTM cells with Z-score ≥ 3.610 ($p < 0.05/327 = p < 0.0001$).

Then, we assessed if the hotspots of the pathway-specific alien species richness and the total alien species richness followed the same spatial distribution. We grouped the hotspots of alien species richness in three sets: total alien species richness, richness across intentional pathways and richness across unintentional pathways. Then, we assessed the intersection among these three sets of hotspots and calculated spatial congruence as the ratio between the number of shared hotspots with the set of total alien species richness and the total number of different hotspots. Additionally, we followed the same procedure with six sets of hotspots: total alien species richness and five sets of pathway-specific alien species richness (one set for each individual pathway).

We performed a redundancy analysis (RDA) to test how environmental variables drive pathway-specific alien species richness (i.e. five response variables consisting in the number of species introduced through each pathway). We standardized the response variables (using the argument scale = TRUE in the rda() function) and the explanatory environmental variables (using the decostand() function). We tested the global result of the RDA and all the canonical axes for significance with a permutation test. To control multicollinearity among the explanatory variables, we computed the variance inflation factor (VIF), which is considered to show acceptable collinearity for VIF < 10 (Borcard et al., 2011). We also computed a Pearson's correlation matrix and prioritized the removal of those variables with high |r| and less ecological sense, until we reached VIF < 10 (the VIF was recalculated after each removal).

We also performed a separate RDA to assess whether results would differ by the inclusion of total alien species richness, but it was discarded as it yielded very similar results (Tables S1.2-S1.3, Fig. S1.2).

All analyses were performed with R-Studio (version 3.6.3; R Core Team, 2020). Cramér's V was calculated with the ‘DescTools’ package (Signorell et al., 2020). Pairwise Tukey contrasts among slopes were performed with the ‘emmeans’ package (Lenth, 2020). The Gi* statistic was calculated with the ‘spdep’ package (Bivand & Wong, 2018). Spatial congruence was assessed via set intersections with the ‘UpSetR’ package (Gehlenborg, 2019). RDA was performed using the ‘vegan’ package (Oksanen et al., 2019). GIS data were extracted and treated using Miramon (version 8.2e; Pons, 2002).

Table 2.2. Number of species introduced for each pathway across taxonomic groups (total number of species = 869). Since some species (N = 43) have been introduced via two pathways, the sum of counts column-wise (43 species are counted twice) doesn’t coincide with the sum of counts row-wise (all species are counted only once). Plants include terrestrial (N = 520) and aquatic (N = 27) species. The corridor pathway was also assessed, but no alien species could be linked to this category.

Group	Release	Escape	Contaminant	Stowaway	Unaided	Total
Aquatic invertebrates	3	6	12	5	0	22
Aquatic vertebrates	21	31	0	0	1	43
Plants	13	375	146	17	17	547
Terrestrial invertebrates	1	1	73	15	14	100
Terrestrial vertebrates	3	150	1	1	6	157
Total	41	563	232	38	38	

2.4. Results

Species range size across pathways and groups

Most alien species were introduced through a single pathway and only 43 out of 869 were introduced through two pathways. Yet, the pathways responsible for the majority of introductions were escape (65%) and contaminant (26%), with similar number of species introduced through the release, stowaway and unaided pathways (Table 2.2). Most alien species had small range sizes (95% of them occupy less than half of our study area; Fig. S1.3).

Alien species introduced through different pathways or belonging to different taxonomic groups generally had a similar (i.e. non-significantly different) range size after considering MRT. There were only two groups of non-overlapping slopes among five different categories in both ANCOVA models (in agreement with extensive overlapping among confidence intervals; Table 2.3; Fig. 2.2).

Among pathways ($R^2_{adj} = 0.351$), the rate of increase in range size was lowest for the unaided and escape pathway, with only the contaminant pathway spreading at a significantly faster rate (all other pairwise comparisons of slopes: p-v > 0.05; Table 2.3, Fig. 2.2). There was extensive overlap in range size between intentional and unintentional pathways; and between unaided and aided pathways, although the unaided pathway was the only one with an almost flat slope (Fig. 2.2).

Table 2.3. Pairwise differences in range size among pathways and taxonomic groups, assessed through Tukey contrasts of the slopes obtained from an ANCOVA model: the effect of pathway and taxonomic group on range size (ln-transformed), using the Minimum Residence Time (MRT) as a continuous covariate (N = 869 species). Plants pool terrestrial (N = 520) and aquatic (N = 27) species.

	Slope	
ANCOVA with pathway		
Contaminant	0.462 ± 0.083	b
Release	0.875 ± 0.462	ab
Stowaway	0.478 ± 0.224	ab
Escape	0.183 ± 0.024	a
Unaided	0.032 ± 0.097	a
ANCOVA with taxonomic group		
Terrestrial vertebrates	2.886 ± 1.822	ab
Plants	0.271 ± 0.029	b
Aquatic vertebrates	1.019 ± 0.43	ab
Aquatic invertebrates	1.421 ± 1.671	ab
Terrestrial invertebrates	-0.002 ± 0.017	a

Slopes were the rate of increase in range size over time (calculated between MRT of 0 and 100, to avoid extrapolating). Slopes were calculated at the scale of the response (undoing the ln-transformation), and are presented with ± 1 standard error. Slopes followed by the same letter did not differ significantly (Tukey contrast: p-v > 0.05).

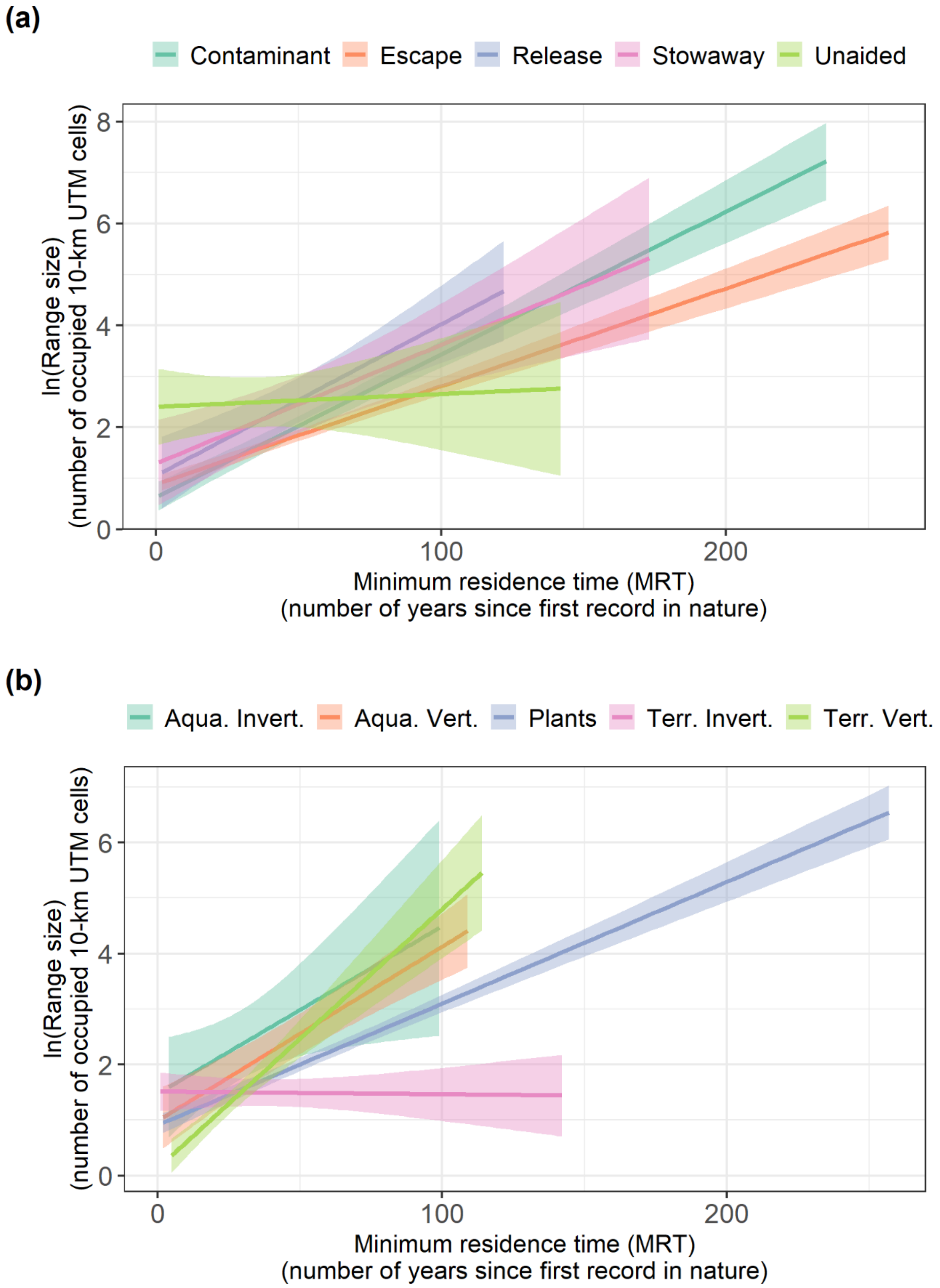


Fig. 2.2. Range size of alien species in Catalonia (N = 869 species) in relation to the MRT for (a) each pathway, and (b) taxonomic group based on the ANCOVA models. Range size is ln-transformed. Shaded area indicates 95% confidence interval around linear regression slopes. Plants pool both terrestrial and aquatic plants. Abbreviations in panel (b): Aqua. = aquatic; Vert. = vertebrates; Invert. = invertebrates.

Among taxonomic groups ($R^2_{adj} = 0.368$), the rate of spread was lowest for terrestrial invertebrates, with only plants spreading at a significantly faster rate (all other pairwise comparisons of slopes: p-v > 0.05; Table 2.3, Fig. 2.2). Indeed, terrestrial invertebrates stood out as being the only taxonomic group with an almost flat slope (Fig. 2.2). Results of additional groupings are presented in Table S1.4.

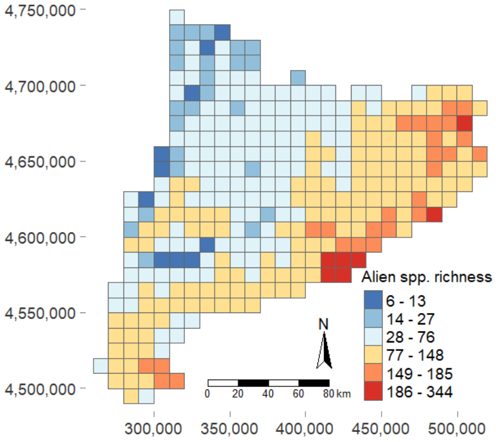
Pathways were associated with taxonomic groups (effect size: Cramer's V = 0.359). The release pathway was comprised mostly of aquatic vertebrates (51%) and plants (31%), while the escape pathway was made up of a majority of plants (66%) and terrestrial vertebrates (26%). In the unintentional pathways (contaminant, stowaway, unaided), most species were either plants (44%–63%) or terrestrial invertebrates (31%–39%).

Spatial patterns and drivers of pathway-specific alien species richness

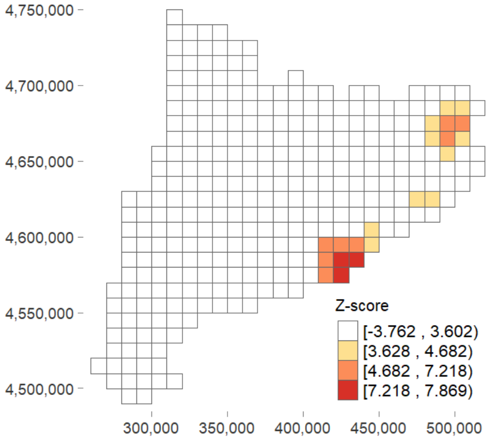
Alien species richness (both total and pathway-specific) was unevenly distributed in our study area, with a total of 67 hotspots, generally located near the coast, on eastern Catalonia, around urban areas, deltas, marshlands and irrigated plains (Fig. 2.3). The urban area around Barcelona was a hotspot for all pathways with an exception for release. Only the release, contaminant and unaided pathways had hotspots on the western half of the study area. There was low spatial congruence between the hotspots of total alien species richness and the hotspots of pathway-specific alien species richness (Fig. 2.4). Congruence with hotspots of total alien species richness was similar between intentional (28%) and unintentional (30%) pathways. Intentionality was not clearly related to congruence (which was overall low) when considering individual pathways. The most congruent pathways were escape (28%) and contaminant (27%). The other pathways showed even smaller congruence with the hotspots of total alien species richness: release (6%), stowaway (19%), unaided (21%).

Fig. 2.3. Alien species richness per 10-km UTM cell, showing richness counts (left) and richness hotspots (right): (a, b) total number (N = 869 species), (c, d) Release (N = 41 species), (e, f) Escape (N = 563 species), (g, h) Contaminant (N = 232 species), (i, j) Stowaway (N = 38 species), (k, l) Unaided (N = 38 species). Maps on the left show counts of alien species richness divided in quantiles (0%-2.5%-10%-50%-90%-97.5%-100%). In the release, stowaway and unaided pathways the lower 2.5% and 10% quantile have the same value, and cells are coloured according to the lower 2.5% quantile. Maps on the right show hotspots of alien species richness as identified by the local Getis-Ord statistic (G_i*), which produces a Z-score. UTM cells with Z-score higher than 3.610 are considered as richness hotspots. This visualization is restricted to 10-km UTM cells with more than 40% of their surface on Catalan land (N = 327 cells). Abbreviations: alien spp. richness = alien species richness.

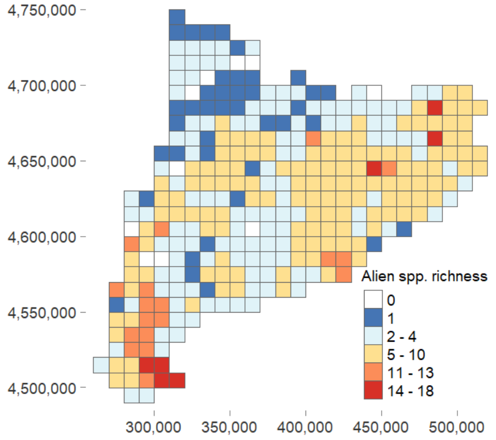
(a) Total (richness counts)



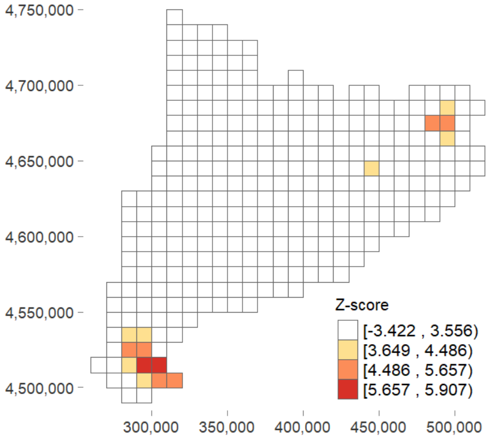
(b) Total (richness hotspots)



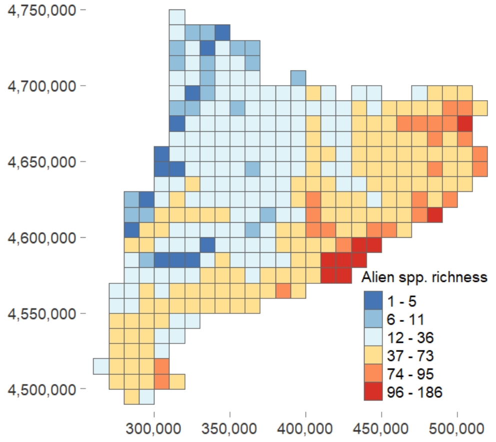
(c) Release (richness counts)



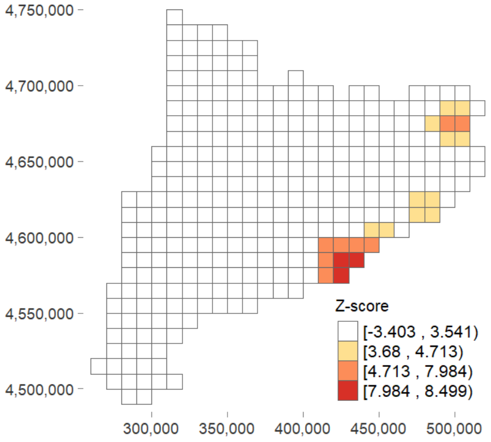
(d) Release (richness hotspots)



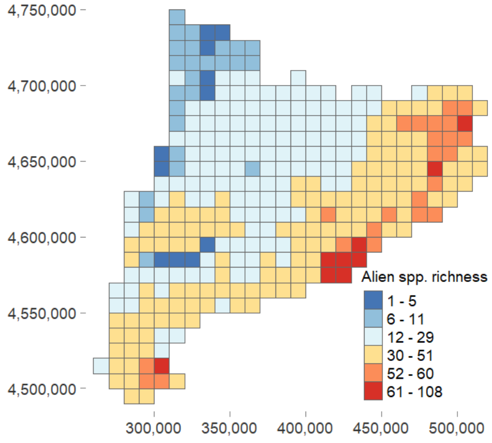
(e) Escape (richness counts)



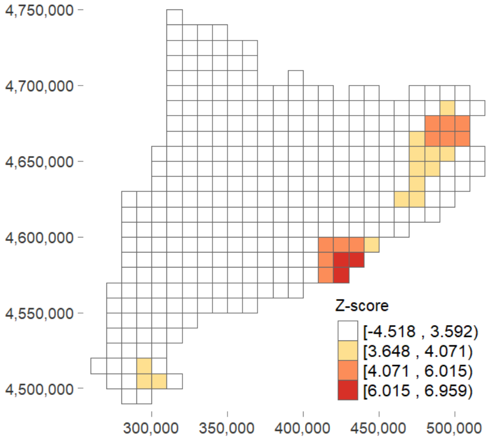
(f) Escape (richness hotspots)



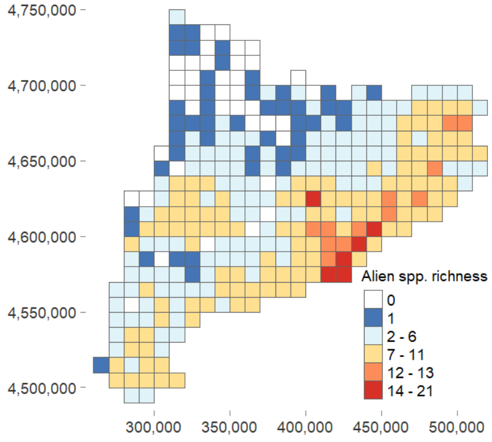
(g) Contaminant (richness counts)



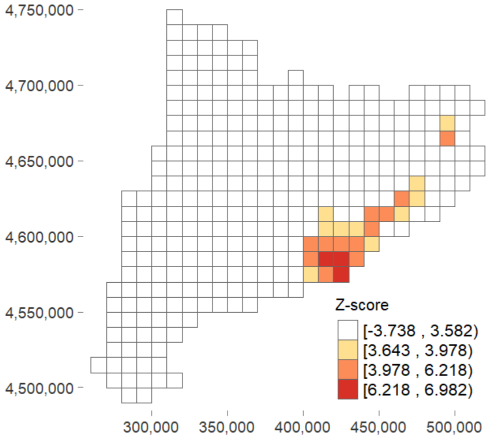
(h) Contaminant (richness hotspots)



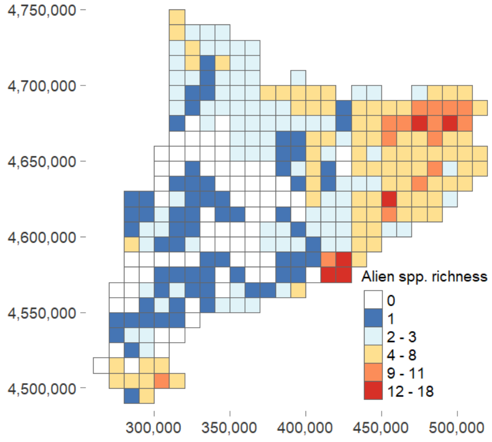
(i) Stowaway (richness counts)



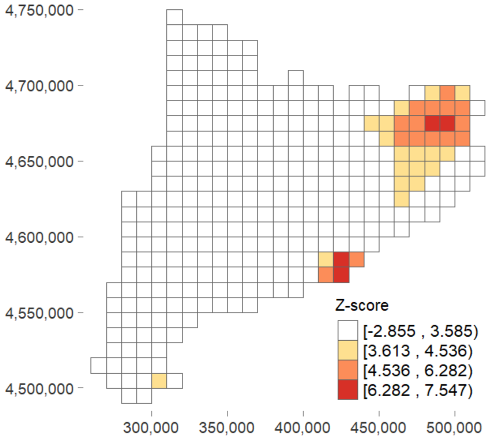
(j) Stowaway (richness hotspots)



(k) Unaided (richness counts)



(l) Unaided (richness hotspots)



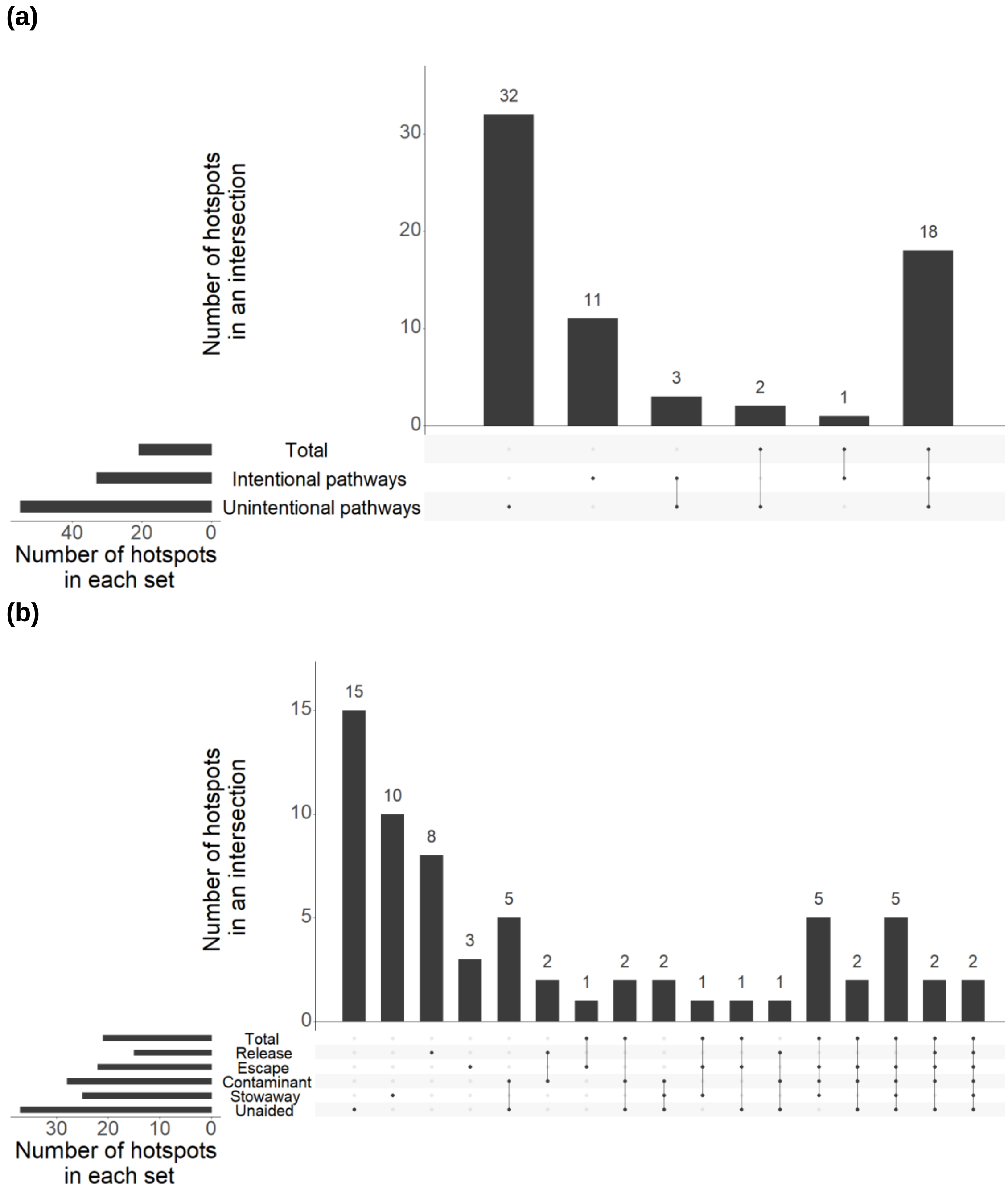


Fig. 2.4. Assessment of spatial congruence through the intersection between sets of hotspots (number of different hotspots = 67), considering total species richness and pathway species richness, either: (a) grouping pathways by intentionality, or (b) considering each individual pathway. The number of sets that participates in an intersection increases from left to right. Intersections with no hotspots are not shown (i.e. it is not shown that no hotspot is exclusive of the contaminant pathway).

RDA showed low collinearity (VIF < 10) with the removal of mean temperature (highly correlated with altitude) and the UTM Y coordinate (highly correlated with the distance to the coast). The RDA was globally significant ($R^2_{adj} = 0.60$, $p < 0.05$), with three significant canonical axes (all significant axes, $p < .05$). Up to 36% of total variation was explained by environmental variables (value corrected with the R^2_{adj}; (Borcard et al., 2011) in the RDA (Tables S1.5-S1.6). Pathway-specific alien species richness was positively related to proxies that pool the effects of colonization and propagule pressure (increasing with greater urban cover and population density, and lesser distance to roads and railroads), and longitude (i.e. the UTM X coordinate); and negatively related to distance to the coast and altitude (Fig. 2.5). The relative strength of these relations was moderately consistent across pathways. Escape richness was most closely related to urban cover, while unaided richness was most closely related to longitude. The remaining richness across pathways was positively related to urban cover, with the strongest relation for contaminant richness, the weakest for release richness and stowaway richness in an intermediate position.

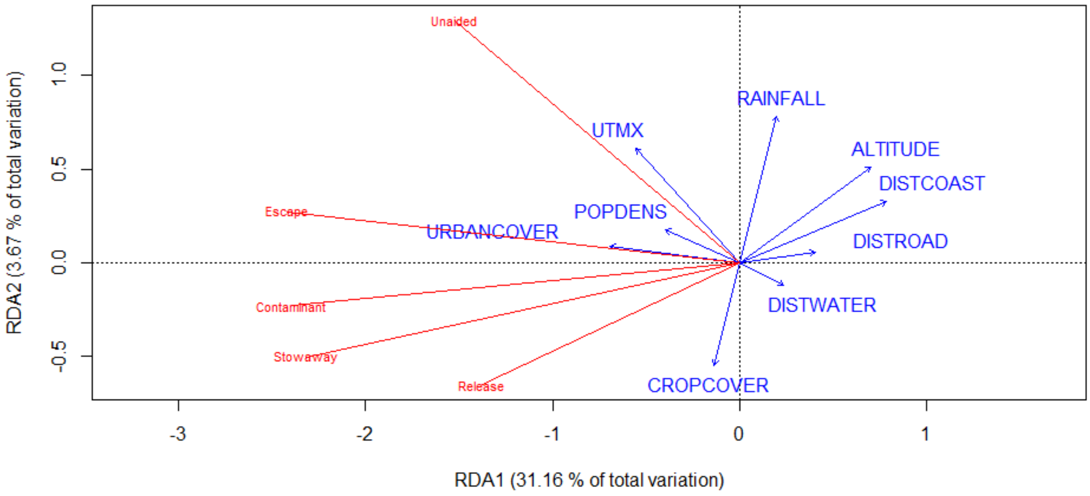


Fig. 2.5. RDA correlation biplot, featuring the first two canonical axes (35% of total variation). Explanatory variables follow the abbreviations in Table 2.1. This analysis is restricted to 10-km UTM cells with more than 40% of their surface on Catalan land (N = 327 cells).

2.5. Discussion

Our study addressed the effect of introduction pathways on the range size of alien species and in the spatial patterns of their richness, across taxonomic groups. Range size was largely equivalent across pathways and taxonomic groups. Pathway-specific nuances in relation to proxies that pooled the effects of colonization and propagule pressure determined low congruence among hotspots of species richness across pathways. Overall, the effect of pathways was such that even if aliens introduced through different pathways spread to a similar extent, they did not accumulate in the same locations.

Species range size across pathways and groups

Unexpectedly, pathways were largely equivalent at determining range size (extensive overlap in range size over time, rejecting H1). Species introduced through the unaided pathway achieved the smallest ranges (almost no increase in range size over time), although their range sizes overlapped with those of the aided pathways. Range size was similar independently of pathway intentionality, with extensive overlap among intentional (release, escape) and unintentional (contaminant, stowaway, unaided) introductions. Our results show similar range size for release, contaminant and stowaway pathways, corroborating those obtained for plants in the Czech Republic (Pyšek et al., 2011), but extending them to both alien vertebrates and invertebrates. Overall, similarities among pathways suggested shared underlying factors that determine range size, although current research on pathways does not provide robust suggestions on underlying mechanisms (especially across taxonomic groups). Previous research supports a similarity between intentional and unintentional pathways, since both introduction types lead to similar variation in genetic diversity across taxonomic groups (in introduced populations compared to native populations; Uller & Leimu, 2011). Nevertheless, this variation has not been linked to invasion success (Uller & Leimu, 2011); hence, variation in genetic diversity among pathways might not be a mechanism for similarities in range size. Another shared feature of pathways may be the preferential transport of widespread and abundant species over rare ones (although with nuances among pathways; Blackburn et al., 2015).

Nuances in the selection of species for transport could explain the lower range of the escape pathway compared to contaminant. Previous work with plants at large scales showed that cultivation led to a greater number of occupied regions (W. Guo et al., 2019; Pyšek et al., 2015). Nevertheless, a study in the Czech Republic showed greater range size for the escape pathway only for plants with a casual status (while naturalized and invasive plants showed similar ranges between escape and contaminant pathways; Pyšek et al., 2011). It has been suggested that unintentional pathways might select higher dispersal abilities that allow plants to associate with either goods or transport vessels (Pyšek, 1998; Pyšek et al., 2011), such as lighter or smaller seeds (von der Lippe & Kowarik, 2012). This is the case for agricultural weeds, which have been introduced unintentionally in the European flora and are among the most widespread alien plants (Pyšek et al., 2009). These dispersal-associated traits that promoted first introduction would also mediate spread in the introduced areas (von der Lippe & Kowarik, 2012). Previous research in our study area found that those alien plants that most increased in range size in recent decades (1990–2012) were introduced unintentionally (Girado-Beltrán et al., 2015). Lack of human aid could explain the low range size for the unaided pathway, as they only benefit from propagule and colonization pressure in the area of introduction from which they spread.

The link between range size and introduction pathways was modulated by taxonomic groups (through the association between groups and introduction pathways; Tables 2.2 and S1.4). This corroborates the idea that the relationship between introduction pathways and invasion success is less straightforward than expected (Faulkner et al., 2016). Similarly to introduction pathways, lack of difference in range sizes among the taxonomic groups suggested shared underlying factors, although research is lacking to provide robust suggestions. Association with introduction pathways may explain the lower range size for terrestrial invertebrates compared to plants. Terrestrial invertebrates and the unaided pathway have a similar trend (Fig. 2.2). Moreover, among all taxonomic groups, terrestrial invertebrates have the highest percentage of species that have spread unaided (15% vs. 3% for plants). Nevertheless, terrestrial invertebrates also have the highest percentage of species introduced as contaminants (70% vs. 26% for plants), so additional factors are probably at play, such as differences in the species' dispersal ability. We note that our data could have underestimated the range size and the MRT of terrestrial invertebrates due to the already known difficulty of detecting unintentionally introduced small species (Rabitsch, 2010a; Roques, 2010).

Differences in pathway frequencies across taxonomic groups suggest that pathways are non-random processes, likely due to the combination of human use and species attributes (Hulme et al., 2008; Saul et al., 2017). The long history of human use of vertebrates and plants for various purposes means that most vertebrates and plants are introduced intentionally (Crosby, 2004; van Kleunen, Essl, et al., 2018). In comparison, human use of invertebrates is very limited, and thus, they are mostly introduced unintentionally (Rabitsch, 2010a). In addition, propagules of invertebrates (eggs or adults) and plants (seeds) are typically smaller than those of vertebrates (individuals) and hence more difficult to detect, with a greater chance of being introduced unintentionally compared to vertebrates (Saul et al., 2017).

Spatial patterns and drivers of pathway-specific alien species richness

Hotspots of pathway-specific alien species richness had low spatial congruence. Similarly to our results with range size, intentionality did not determine clear-cut differences across pathways (thus contradicting H2). Moreover, our results confirmed the key role of proxies that pool the effect of colonization and propagule pressure (urban cover, population density and distance to roads) at increasing pathway-specific alien species richness (except for the unaided pathway, largely supporting H3). Yet, the strength of the relationship was uneven across pathways. Nuances in the relationship between pathways and environmental drivers might explain the low congruence among hotspots: if factors determining invasion risk slightly differ among pathways, a site at high risk of invasion from one type of activity (e.g. gardening) might not be at high risk of invasion from other activity (e.g. deliberate release). We note that patterns of alien species richness (number of species occupying a site) are interrelated with range size (number of sites occupied by species; Blackburn et al., 2020). Therefore, the insights from the relationship among pathways and range size will also contribute to understanding the processes behind the spatial pattern with low congruence.

As mentioned above, uneven relationship among pathway-specific species richness and populated areas suggested that the risk of invasion is not determined in the same way across pathways. Urban areas concentrate gardening activities and pet ownership, explaining the close relation with escape species richness, but they are also focus of global trade and movement of people (Early et al., 2016). For instance, during 2009, 80% of tourism in our study area concentrated in the city of Barcelona and coastal areas (Llurdés et al., 2009). Contaminants reach these urban areas with particular commodities, while stowaways can be introduced by transport vessels themselves (airplanes, ships) or travel in luggage (Harrower et al., 2018; Rabitsch, 2010a). Nevertheless, contaminants and stowaways spread beyond population centres to a greater extent than escapes (on account of their larger range size), and this contributes to low spatial congruence and weaker association with urban areas. In addition to trade and tourism, the introduction of contaminants is also related to agricultural activities (e.g. through contaminated seeds; Harrower et al., 2018), which further explains the lower association with population centres. Indeed, intentional introductions are more prominent than unintentional ones in cities worldwide (Padayachee et al., 2017). Stowaways are less related to urban areas than contaminants, most likely because they are not ecologically associated with commodities (unlike contaminants; Harrower et al., 2018), and thus are more likely to detach from transport vessels (Gippet et al., 2019).

The release and unaided pathways showed the weakest relationship with populated areas. In the case of the release pathway, results suggest reduced importance of urban areas in favour of freshwater ecosystems. Indeed, there is no hotspot in the Barcelona conurbation, and over 70% of hotspots coincide either with a reservoir or with river systems in western parts (Catalan Water Agency, 2005). Furthermore, over 60% of released species were aquatic. The large range size of released species suggests that freshwater ecosystems have been targeted extensively in our study area, which is supported by previous works showing ongoing introduction of fish in north-eastern basins and subsequent translocation west-wards into other basins (Clavero & García-Berthou, 2006; García-Berthou et al., 2005). We suggest that the concentration of the unaided pathway in the eastern part of Catalonia is related to the partial barrier effect of the Pyrenees (Martínez & Montserrat, 1990) and the proximity to France. The majority of species of this pathway have spread from this country (Appendix S1) through a lowland coastal corridor in NE Catalonia (e.g. *Myocastor coypus*; Palazón et al., 2015). This corridor has also been involved in the spread of invasive nematodes from the Iberian Peninsula to France (Haran et al., 2015). We also note that the presence of an invasion hot spot in the city of Barcelona (far from political borders) is possibly due to higher sampling effort in the urban area surrounding Barcelona (Pino et al., 2005).

We finally acknowledge that we did not account explicitly for other factors affecting range size and patterns of alien species richness, mainly species attributes (such as dispersal capacity) and environmental factors (such as climate matching), and features of the introduction process explored in the study (such as pathways and minimum residence time). Despite the importance of this interplay according to previous literature (Dyer et al., 2016; Procheş et al., 2012; Wilson et al., 2007), its assessment would have been unfeasible in our study given the diverse assembly of the studied species and the incomplete knowledge of their biological attributes.

Implications for management

Our work has explored how a standardized classification of pathways can be used in conjunction with spatially and temporally explicit databases of alien species (such as EXOCAT), to yield new insights on the role of introduction pathways in shaping biological invasions and to inform management.

Following the prioritization framework of McGeoch et al. (2016), we outline contributions to the prioritization of pathways and joint prioritization of pathways x sites. Since most pathways were relatively equivalent at determining range size, they were of limited use for prioritization in our study area. Nevertheless, since not all widespread aliens are associated with negative impact (Pyšek et al., 2009), this prioritization could be fine-tuned by assessing the numbers of harmful aliens associated with each pathway (McGeoch et al., 2016). Management efforts could target priority sites (i.e. hotspots), and these sites could be monitored for the early detection of new introductions. The prioritization of high-risk areas through the identification of hotspots could be carried out in other countries to enhance preventive management. Moreover, management efforts aiming at reducing sources of propagule and colonization pressure (the main environmental drivers increasing alien species richness) should target priority sites across pathways. Such preventive management efforts should build on pathway-specific nuances in the association with environmental drivers. Management efforts for the escape, contaminant and stowaway pathways could target urban areas (since they concentrate pet ownership, gardening activities, trade and tourism). Efforts targeting the release pathway could concentrate on freshwater ecosystems, and the unaided pathway could consider biogeographical barriers.

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Chapter 3

Effect of introduction pathways on the invasion success of non-native plants along environmental gradients

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3.1. Abstract

Our understanding on the role of introduction pathways on plant invasions is incomplete because their interaction with other factors remains poorly studied. We contributed to filling this knowledge gap, by analysing temporal trends in pathway importance, pathway-specific differences in the invaded niche, and the effect of pathways on invasion success. We used the non-native flora of Catalonia (NE Spain) as a study system. The contribution of pathways to the non-native flora interacted with time: from before 1500 to the present, gardening replaced agriculture as the main donor of new plants, while the contribution of unintentional introductions fluctuated without a consistent trend. Among neophytes (plants introduced after 1500), introduction pathways influenced differences mainly in habitat type, and secondarily in elevation: natural habitats and high elevation promoted invasion by gardening plants over unintentionally introduced ones. These nuances were unrelated to interactions between environmental variables. Among neophytes, invasion success was unrelated to pathways and interactions between pathways and traits, but was positively related to minimum residence time: older introductions achieved greater area of occupancy, habitat range, and invaded climatic niche breadth. Our results suggest that non-native plants diversified their niches over time (1500-present), a process that resulted in similar area of occupancy and niche breadth across plants with different introduction pathways. This was accompanied by pathway-specific nuances in the type of invaded environmental conditions.

3.2. Introduction

Human socioeconomic activity is currently re-shaping the distribution of species through the intentional and accidental transport of species beyond biogeographic barriers (W. Dawson et al., 2017; Pyšek et al., 2017). For non-native plants, such introductions occur via gardening, agriculture, forestry, and the global exchange of commodities and people (Kowarik & von der Lippe, 2007; van Kleunen, Essl, et al., 2018). This diversity of human socioeconomic activities that introduces non-native species has been categorized into the so-called introduction pathways (Harrower et al., 2018; Hulme et al., 2008; Richardson et al., 2011). Pathways influence the assembly of non-native floras (i.e. the accumulation over time of non-native plants in a recipient territory; Essl et al., 2015; Seebens et al., 2022); the invaded niche (i.e., the invaded environmental conditions in the invaded area; González-Moreno et al. 2013; Donaldson et al. 2014); and the invasion success of non-native plants (i.e., the ability of a non-native plant to overcome barriers to invasion; Riera et al., 2021; Thuiller et al., 2012; van Kleunen et al., 2020). However, it remains poorly known how pathways interact with intrinsic (e.g. species' traits) and socioenvironmental factors in shaping species' invasion over space and time (Pyšek et al., 2020). Filling these knowledge gaps is important because a better understanding of how pathways influence the invasion process is required to meet conservation targets, and prioritize pathways associated with greatest negative impact (Essl et al., 2015; McGeoch et al., 2016). Pathways are a key element in the management of biological invasions, as they offer an opportunity for the preventive management and early warning of new invaders (Convention on Biological Diversity, 2014; McGeoch et al., 2016).

The relative contribution of pathways to the assembly of non-native floras has shifted over time, following socioeconomic changes, such as the globalization of trade routes and substantial exchange of plants among continents (Arianoutsou et al., 2021; Faulkner et al., 2016; Hulme et al., 2008; Lambdon et al., 2008b; Wilson et al., 2009; Zieritz et al., 2017). One of the consequences of such socioeconomic changes is that in recent centuries (from 1500 onwards), gardening has replaced agriculture as the dominant source of new non-native plants (Cerrato et al., 2023; Dodd et al., 2015; Lehan et al., 2013; Mack & Lonsdale, 2001; Pyšek et al., 2003; Sanz-Elorza, Mateo, et al., 2009; Seebens et al., 2022). Yet, we know little about whether these replacement dynamics hold if we include plants introduced before the onset of extensive floristic exchange among continents (before 1500; Dehnen-Schmutz, 2004). Such assessment could provide guidance for regions going through increasing globalization, which could be prone to mirror introduction patterns (Cerrato et al., 2023; Q. Guo et al., 2017).

The relationship between introduction pathways and the invaded niche relates to pathway-specific differences in the type of invaded environmental conditions, encompassing land use, climate and topography among other factors (Carboni et al., 2011; Donaldson et al., 2014; Thuiller et al., 2006). In particular, since land use approximates the type of human activity (Donaldson et al., 2014; González-Moreno et al., 2013; Riera et al., 2021), land use is expected to have an effect on propagule pressure (total number of introduced individuals across introduction events; Lockwood et al. 2005) in a pathway-specific way. For example, urban land use would concentrate introduction epicentres (initial foci of introduction and spread; Early et al., 2016) for gardening introductions (e.g. public and private gardens; Padayachee et al., 2017; Riera et al., 2021). In contrast, agricultural land use might concentrate introductions of accidentally introduced weeds (e.g. crop seed contaminants) and escaped crops (González-Moreno et al., 2013; Kowarik & von der Lippe, 2007; Lehan et al., 2013). Pathway-specific differences in the invaded niche also relate to elevation, since non-native plants introduced through different pathways react differently to land use, anthropogenic disturbance, and transport infrastructure along elevation gradients (Akatova & Akatov, 2019; Alexander et al., 2016; McDougall et al., 2011). Previous work suggests that this relationship is context dependent: gardening plants became less prevalent with increasing elevation in mountain regions worldwide (McDougall et al., 2011) and in the Western Caucasus (Akatova & Akatov, 2019), while an opposite pattern was reported in Central Europe (Chytrý et al., 2021) and South Africa (Thuiller et al., 2006). Moreover, pathway-specific differences in the invaded niche also relate to historical landscape (in coastal habitat patches; Başnou et al., 2015), and the availability of dispersal corridors (roads and streams, in Mediterranean forest edges; González-Moreno et al., 2013), giving complex invasion patterns. Despite this knowledge, whether land use and elevation interact to define pathway-specific differences in the invaded niche has not been tested before (to the best of our knowledge).

Invasion success depends not only on introduction pathways and environmental conditions, but also on the non-native plant's traits and attributes (Casado et al., 2018; Gallagher et al., 2015; Pyšek et al., 2020; Pyšek & Richardson, 2007). Invasion success is frequently measured via proxies such as geographical spread and niche breadth (Riera et al., 2021; Thuiller et al., 2012; van Kleunen et al., 2020). For example, geographical spread has been related to plant's growth form and height, a proxy of a plant's ability to acquire resources and life cycle span (Fristoe et al., 2021; Giulio et al., 2020; Lazzaro et al., 2020; Pyšek et al., 2017). Dispersal (through seed or asexual reproduction) is also crucial in geographical spread (Fristoe et al., 2021; Gassó et al., 2009; Moyano et al., 2022), and plants with a wide climatic niche in their native range are likely to invade a wide breadth of climatic conditions in their non-native range (Castro-Díez et al., 2011).

While not a plant trait per se, the time since the first record outside of cultivation (minimum residence time) has also been identified as an important correlate of the breadth of the invaded climatic niche (Banerjee et al., 2021), habitat range (Lazzaro et al., 2020; Pyšek et al., 2011), and of geographical spread (Fristoe et al., 2021; Riera et al., 2021). Such plant attributes have mostly been tested without accounting for interactions with introduction pathways (Moyano et al., 2022), although previous work found evidence of an interaction between introduction pathways and minimum residence time (Pyšek et al., 2011; Riera et al., 2021). Therefore, whether the effect of trait characteristics on invasion success can be amplified or reduced, by the way in which the plant was introduced, remains poorly understood.

In this paper, we tested: (i) changes over time in the contribution of pathways to the assembly of a regional non-native flora; (ii) how these introduction pathways shape the invaded niche of non-native plants; (iii) how the interaction between pathways and plant traits shapes their invasion success in terms of area of occupancy, habitat range, and invaded climatic niche breadth. Specifically, we addressed the following hypotheses: (H1) Over the past millennium (from before 1500 to the present), we expected gardening to replace agriculture as the main contributor to the non-native flora, as reported in shorter timescales due to well known-socioeconomic changes (Dehnen-Schmutz, 2004; Pyšek et al., 2003; Sanz-Elorza, Mateo, et al., 2009). (H2) Urban land use would promote invasion by gardening plants over unintentionally introduced ones, based on the expectation that introduction epicentres for each pathway are related to the land use (Donaldson et al., 2014; González-Moreno et al., 2013; Riera et al., 2021). (H3) Non-native plants introduced through gardening would invade lower elevations than those introduced unintentionally (McDougall et al. 2011; Akatova and Akatov 2019, but see: Chytrý et al., 2021; Thuiller et al., 2006). (H4) The relationship between pathways and elevation would be affected by land use, with increasing urban use favouring gardening plants. (H5) Introduction pathways would interact with minimum residence time, with unintentionally introduced plants becoming more successful over time compared to those introduced through other pathways (Riera et al., 2021).

3.3. Methods

Study area

We used the non-native flora of Catalonia (NE Spain) as a study system, since there is substantial information of the non-native flora of this Mediterranean region (Andreu & Pino, 2013; Aymerich & Sáez, 2019a; Casasayas, 1989; Clotet et al., 2016; Rotchés-Ribalta et al., 2021). We considered the overall region (32,000 km^2; 7.7 million inhabitants), and the sub-regional administrative unit of the Barcelona province (7,726 km^2; 5.5 million inhabitants; Fig. 3.1). Catalonia is bounded by the Mediterranean coast in the East, and by the Pyrenees in the North. The region shows several climatic gradients, with increasing temperature and decreasing precipitation towards the South, and dry inland conditions compared to moist and temperate climates near the coast (Ninyerola et al., 2000). The Catalonia region includes the Barcelona province, which contains diverse ecosystems, mostly Mediterranean, but also encompassing temperate, sub-alpine and alpine environments (Clotet et al., 2016). Both Catalonia and the Barcelona province have endured substantial land use changes since the 19th century: important decrease of forested areas and croplands, in favour of residential, industrial, and commercial development. Moreover, population density increased along the coastline, in the Barcelona city and its conurbation (Başnou et al., 2015; Ibàñez & Buriel, 2010). All these factors have favoured the spread of non-native plants (Clotet et al., 2016; Pino et al., 2005).

Data gathering and variables definition

To test our five hypotheses, we classified non-native plants into three pathway categories: (1) agriculture and forestry (plants introduced for cultivation to provide food or timber); (2) gardening (plants introduced for cultivation as ornamentals or for medicinal use); and (3) unintentional (plants introduced accidentally with the sowing of contaminated seed lots, global trade and tourism). Such pathway classification was based on previous work on the non-native flora of Catalonia (Aymerich & Sáez, 2019a;

Riera et al., 2021; Rotchés-Ribalta et al., 2021). These categories were not mutually exclusive: a non-native plant could have been introduced through more than one pathway. Our categories matched those of Hulme et al. (2008) as follows: “agriculture/forestry” and “gardening” related to subcategories of the Escape pathway, while “unintentional” combined the pathways Contaminant and Stowaway. Agriculture, forestry, and gardening plants encompassed plants with economic use (van Kleunen et al., 2020). We did not include other pathways (release, corridor, unaided) of the Hulme et al. (2008) framework, as these represented around 4% of all non-native plants in our study area (Riera et al., 2021; Rotchés-Ribalta et al., 2021). However, a plant introduced through the “release” pathway was kept if it had also been introduced for gardening, and was classified to the “gardening” pathway.

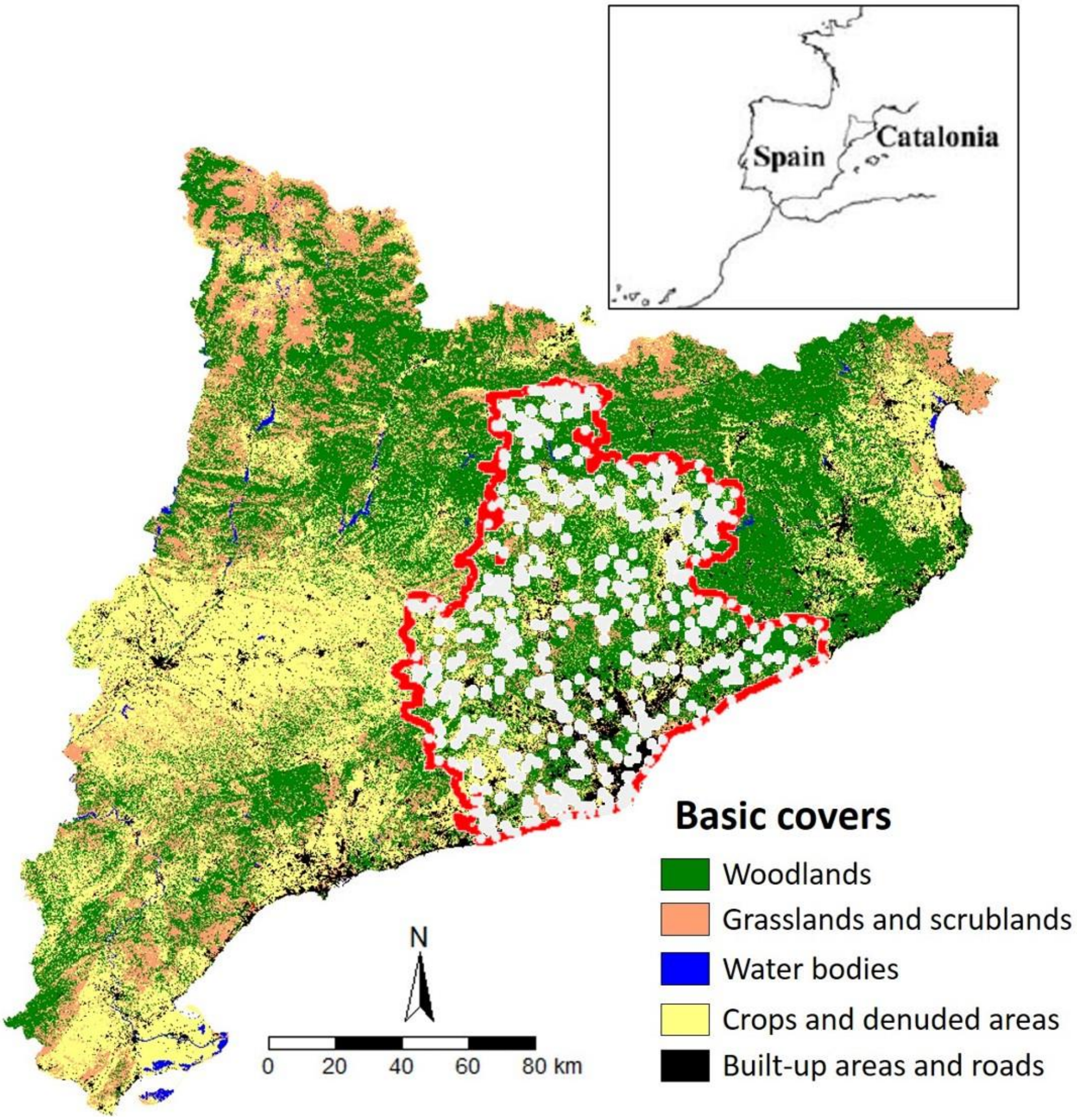

Fig. 3.1. Land-cover map of Catalonia, generalized from the land-cover map of 2009 (http://www.creaf.uab.cat/mcsc/), with the Barcelona province outlined in red, and sampling points in light grey.

Table 3.1. Potential drivers of pathway-specific differences in the invaded niche, which we approximated through the proportion of plants introduced through gardening. N = 190 invaded plots (Barcelona province). Abbreviations = CREAF = Centre for Ecological Research and Forestry Applications, EPSG = European Petroleum Survey Group.

Variable (units)	Data source
Land use	
Habitat type (categorical)*	Field sampling (CREAF)
Urban land-cover 2009 (%)*	Land-cover Map of Catalonia, CREAF (2009); http://www.creaf.uab.cat/mcsc/
Cropland land-cover 2009 (%)*	
Climate	
Mean annual temperature (°C)	World Clim v2.1 (1970-2000)
Mean annual solar radiation (kJ m^{-2} day^{-1})	
Annual precipitation (mm)	
Topography	
Latitude (m)	EPSG:25831
Longitude (m)*	
Elevation (m)*	Digital Elevation Model of Catalonia
Distance to nearest main stream (m)*	Catalan Water Agency; http://aca.gencat.cat/ca/laigua/consulta-de-dades/descarrega-cartografica
Distance to nearest main road (m)*	Catalan Government; http://sig.gencat.cat/visors/CatalegCarreteres.html
Historical landscape	
Cropland land-cover 1956 (%)	Land-cover Map of Catalonia, CREAF (1993), Land-cover Map of Barcelona Province, CREAF (1956); http://www.creaf.uab.cat/mcsc/; http://www.sitxell.eu/ca/mapa_historics.asp
Urban land-cover 1956 (%)	
Cropland land-cover 1993 (%)	
Urban land-cover 1993 (%)	
Historical landscape changes	
Progressive changes in 1956-2009 (%)	Land-cover Map of Catalonia, CREAF (1993), Land-cover Map of Barcelona Province, CREAF (1956); http://www.creaf.uab.cat/mcsc/; http://www.sitxell.eu/ca/mapa_historics.asp
Regressive changes in 1956-2009 (%)*	
No changes in 1956-2009 (%)*	
Progressive changes in 1993-2009 (%)	
Regressive changes in 1993-2009 (%)	
No changes in 1993-2009 (%)	

* Variables selected for the binomial GLM models

To address whether over the past millennium (before 1500-2019), gardening would replace agriculture as the main contributor to the non-native flora (H1), we used the recent checklist of the non-native flora of Catalonia, which included archaeophytes (plants introduced before 1500; Aymerich & Sáez, 2019a). We removed doubtful occurrences, intergeneric hybrids, and hybrids thought to have originated in our study area, yielding a selection of 1025 non-native plant species. We classified plants into the three above-mentioned introduction pathways. We note that 21 plants were introduced through two pathways, so they were duplicated in the database. We also classified plants into the following, expert-defined introduction periods: (1) before 1500 (previous to large-scale intercontinental trade, including the Middle Ages, Antiquity, and Prehistory); (2) 1501-1900 (increase in intercontinental trade, onset of industrialization); (3) 1901-1984 (strong industrialization, population increase and concentration in urban areas, onset of the "Great acceleration" in globalization; Lewis & Maslin, 2018); and (4) 1985-2019 (accession of Spain to the European Union, increase in research interest into non-native plants, and further increase in intercontinental trade and concentration of population in urban areas). Such classification was based on the year of first record outside of cultivation (obtained mainly from Riera et al. (2021), except for plants introduced before 1500 (their introduction period was taken directly from Aymerich & Sáez (2019a).

To address the remaining hypotheses, we used data from a field sampling covering the Barcelona province (year of sampling: 2012; Clotet et al., 2016). Sampling plots (N = 632) were selected at random and stratified on a digital layer of the ten most widespread habitat types in the Barcelona province (https://www.ub.edu/geoveg/en/semhaveg.php). Then, presence and abundance of neophytes (plants introduced after 1500) were recorded in a radius of five meters around each point. Native species were not sampled because previous research found no consistent association between the richness of non-native and native plants (Vilà et al., 2007). Overall, we obtained data on the presence of 77 non-native plans, across 190 invaded plots.

To test pathway-specific differences in shaping the invaded niche (H2-H4), we calculated the proportion of gardening plants per plot (out of the sum of gardening + unintentional), and modelled this proportion against environmental variables that defined the invaded niche (N = 190 invaded plots). Thus, we could test how environmental conditions promoted invasion by gardening plants over invasion by unintentionally introduced ones. We defined the niche with a selection of the following environmental variables (Table 3.1): habitat type, urban land-cover (2009), cropland land-cover (2009), elevation, climate (mean annual temperature, mean annual solar radiation, annual precipitation), topography (latitude, longitude, distance to nearest main stream, distance to nearest main road), historical landscape (cropland and urban land-cover in 1956 and 1993) and historical landscape changes (progressive, regressive and no changes; for the periods 1956-2009 and 1993-2009). Habitat type included ten categories (which we summarised into three for analysis, see next section): urban, cropland, coastal, broad-leaved forests, coniferous forests, meadows, riparian, rock outcrops, scrublands, and wetlands. The use of urban and cropland land-cover was complementary to the use of urban and cropland habitat type. Habitat types provided information at the local scale on the type of human activity, disturbance regime and vegetation structure of the plot. In comparison, land-cover provided information on the matrix in which the plot was embedded (i.e. which type of human activity, disturbance regime and vegetation structure surrounded the plot). We included distance to streams and roads, and historical landscape, since these landscape features can promote invasion (Başnou et al., 2015; Chytrý et al., 2008; von der Lippe & Kowarik, 2012), and previous work in our study area has suggested pathway-specific differences (Başnou et al., 2015; González-Moreno et al., 2013). We included longitude and latitude to account for spatial dependence, and longitudinal gradients of greater human activity towards the East (outlined in previous work; Clotet et al., 2016; Pino et al., 2005). We also included climatic variables because they are important drivers of plant invasions, as shown by previous work in our study area (Pino et al., 2005). Current and historical land-cover were calculated in buffers of 50, 500 and 1000 meters around the sampling point (urban and cropland land-cover in 1956, 1993 and 2009). We only included land-cover variables calculated in 50-m buffers in analyses because this size was the most coherent with the size of the plots (i.e. it would not include overly remote areas), and we found no significant effect of buffer size on land-cover values (Table S2.1). Then, historical landscape change was also calculated in 50-m buffers (see Appendix 2 Supplementary Methods). Natural land-cover categories were not included as their coverage percentage depends on urban and cropland land-cover. All data was taken from field sampling or publicly-available databases (Table 3.1; Clotet et al., 2016). We did not model non-native plants introduced through agriculture and forestry (N = 20 invaded plots), because they were very infrequent compared to gardening (N = 117) and unintentionally introduced plants (N = 145). Instead, we illustrated pathway-specific niche differences of plants introduced through agriculture and forestry through descriptive statistics of their proportion (in relationship to the total number of non-native plants), across habitats.

To address whether unintentionally introduced plants would become more successful over time compared to those introduced through other pathways (H5), we calculated invasion success in the Barcelona province. We used three complementary variables for all unintentionally and intentionally introduced plants: area of occupancy, habitat range and invaded climatic niche breadth (N = 77 non-native plants; Fig. S2.1). Area of occupancy was the number of invaded 10-km grid cells, calculated through the overlay of a regular grid over occurrence coordinates (Martín-Forés et al., 2023). To minimize the effect of geometric uncertainty, we varied grid origin systematically over multiple iterations, and stored the smallest area of occupancy (the process stopped when the value did not decrease after five iterations, 'redlistr' package; Lee et al., 2019). We obtained similar results with grid cells of 1-km and 2-km (Pearson's r > 0.98, for all pairwise correlations). Habitat range was the count of invaded habitat types (ten categories). Invaded climatic niche breadth was the spread of temperature, precipitation, and solar radiation conditions invaded by non-native plants, in units of standard deviations. We downloaded mean annual temperature (bio1), annual precipitation (bio12), and mean annual radiation, from WorldClim v2.1 (Fick & Hijmans, 2017), at a resolution of 2.5 arc-minutes ('geodata' package; Hijmans et al., 2023). We extracted climate values on occurrences of non-native plants in the Barcelona province with the 'terra' package (Hijmans, 2023). Then, we calculated a principal component analysis ('factoMineR' package; Lê et al., 2008), calculated the standard deviation of the scores of the first two axes, and aggregated the resulting two values with the geometric mean (Palma et al., 2021). Non-native plants present in a single plot were assigned a value of zero. We then gathered data on introduction pathways (gardening, unintentional, agriculture and forestry), minimum residence time, and five plant traits selected for their potential relevance at explaining invasion success (Casado et al., 2018; Castro-Díez et al., 2011; Fristoe et al., 2021; Gassó et al., 2009; Lazzaro et al., 2020): dispersal syndrome, vegetative reproduction, height, growth form and native niche breadth (Table 3.2). Introduction pathway and minimum residence time were taken from this work, and plant traits were taken from various sources (Bolòs et al., 2005; Brummitt, 2001; Castroviejo, 1986–2012; GBIF, 2023; POWO, 2022; Recasens & Conesa, 2003; Royal Botanic Gardens Kew, 2020; Sanz-Elorza et al., 2004a; USDA & NRCS, 2020).

Table 3.2. Potential drivers of invasion success of non-native plants in the Barcelona province (area of occupancy, habitat range and invaded climatic niche breadth). N = 81 (77 non-native plants, four duplicated since they were introduced through two pathways). Abbreviations: CV = coefficient of variation (ratio of standard deviation to mean).

Variable	Type (units)	Details
Introduction pathway	Categorical	Mechanism responsible for the introduction of the non-native plant: agriculture and forestry (N = 9), gardening (N = 42), unintentional (N = 30).
Minimum residence time	Continuous (years)	Number of years that the plant is known from outside cultivation (2012 – year of first record outside of cultivation; range: 6-250, mean = 94.98, CV = 0.66
Dispersal syndrome	Categorical	Mechanism that dispersed seeds away from the parental plant: wind-dispersed (N = 18), animal-dispersed (pooling ecto- and endozoochorous dispersal; N = 21), and unspecific (N = 42). When the syndrome was not stated in the literature, we inferred it from the presence of structures on seeds that facilitate dispersal.
Vegetative reproduction	Categorical	Whether asexual vegetative reproduction is present in a species: yes (N = 35) or no (N = 46).
Height	Continuous (meters)	Maximum height reported in floras, to maximize the probability of representing sexually mature adults (range = 0.04-40, mean = 5.06, CV = 1.45).
Growth form	Categorical	Combination of longevity and growth habit: annual forbs and grasses (N = 24), perennial forbs and grasses (including perennial vines, N = 30), perennial shrubs and trees (including perennial succulents, N = 27).
Native niche breadth	Continuous (standard deviations)	Breadth of climatic conditions in the native range, with the same methodology as invaded climatic niche breadth (range = 0.262-1.248, mean = 0.752, CV = 0.32). Occurrence data from GBiF (GBIF, 2023), see Supplementary Methods (Appendix 2) for data cleaning procedure. Native range from Plants of the World Online webpage (POWO, 2022).

Statistical analyses

To test H1, we gathered a two-way contingency table to assess temporal trends in the relative contribution of each introduction pathway to the assembly of the non-native flora of Catalonia (Table S2.2). To assess the strength of the temporal trends, we calculated significance (Chi-square test) and effect size (Cramér's V, 'DescTools' package; Signorell & mult. al., 2022) of the interaction between introduction pathway and introduction period.

To test H2-H4, we modelled the proportion of non-native plants introduced through gardening in relation to environmental variables defining the invaded niche (in the Barcelona province), by fitting Generalized Linear Models (GLMs) with binomial distribution (logit link). We set the explanatory variables as habitat type, urban land-cover, cropland land-cover, climate, topography, historical landscape and historical landscape changes (Table 3.1). To improve model fit, we reclassified the original ten habitat types into three categories: urban, cropland and natural (pooling the remaining eight categories). This was necessary because five of the "natural" habitats were represented by five or less invaded plots (see descriptive statistics in Table 3.3). While some of the "natural" habitats might have been associated with anthropogenic disturbance over long time periods (i.e. "semi-natural habitats"; Arianoutsou et al., 2013), we refer to them as "natural" for simplicity. To control multicollinearity, we removed variables with high pairwise Pearson's correlation ($|r| > 0.75$; Table S2.3), and those with less ecological meaning, till we achieved variance inflation factors below five ('performance' package, Lüdecke et al., 2021). We removed precipitation, temperature, and latitude, as they were correlated to elevation (all Pearson's $r \geq 0.6$). Mean annual radiation was correlated to longitude ($r = -0.81$). Land-cover was correlated across the years (1956, 1993, 2009; all $r \geq 0.6$), so we kept the most recent data in the models (2009). Likewise, historical landscape change between 1993-2009 was correlated to historical change between 1956-2009 (all $r > 0.45$), so we kept the variables describing a longer time period. In order to obtain comparable coefficients, we standardized the numerical predictors to a mean of zero and standard deviation of one (Schielzeth, 2010). After standardizing, we fitted quadratic terms for cropland land-cover (2009), distance to streams, regressive changes (1956-2009) and no changes (1956-2009), because they improved a model with a standardized linear term (95% confidence interval of the quadratic term did not overlap zero, Akaike Information Criterion corrected for small sample sizes [AICc] decreased, Table S2.4). We fitted the interactions: habitat type x elevation, elevation x urban land-cover (2009 values), and elevation x cropland land-cover (2009 values). Regardless of whether interactions were fitted, our full models fitted the data (likelihood ratio test: $p\text{-v} < 0.01$), were not biased by spatial autocorrelation (low Moran's I of deviance residuals, Fig. S2.2, 'ncf' package; Bjornstad, 2022), and did not show relevant overdispersion (dispersion ratio < 1.07, $p\text{-v} > 0.2$; Lüdecke et al., 2021). We approximated explained variance through McFadden's pseudo-R^2 (Luchman, 2014).

Table 3.3. Overview of pathway-specific differences in the invaded niche, related to habitat type. The proportion of plants introduced through gardening was averaged from the proportion of gardening plants per plot (i.e. they do not come from the binomial GLM shown in Fig. 3). We note that non-native plants introduced through agriculture and forestry were never the only invaders in a plot. Habitats were sorted by increasing proportion of gardening plants. N = 190 invaded plots (out of 632 sampled plots in the Barcelona province). Abbreviations: gard. = gardening, unint. = unintentional, agri/forest = agriculture and forestry.

Habitat	Number of invaded / sampled plots	Mean % of gard. plants	Mean number of gard. plants (range)	Mean number of unint. plants (range)	Mean number of agri/forest plants (range)	Mean total number of non-native plants (range)
Rock outcrops	1 / 57	0.0	0 (0-0)	1 (1-1)	0 (0-0)	1 (1-1)
Croplands	50 / 92	17.8	0.4 (0-2)	1.7 (0-4)	0.1 (0-2)	2.1 (1-6)
Urban	54 / 65	29.1	0.8 (0-4)	1.9 (0-7)	0 (0-1)	2.8 (1-10)
Meadows	5 / 39	33.0	0.8 (0-2)	1.8 (0-3)	0 (0-0)	2.6 (1-5)
Scrublands	3 / 106	44.4	0.7 (0-1)	1 (0-2)	0 (0-0)	1.7 (1-3)
Coastal	16 / 29	54.3	1.4 (0-4)	1.2 (0-4)	0.1 (0-1)	2.7 (1-6)
Riparian	32 / 61	54.6	1.1 (0-3)	1.5 (0-5)	0.4 (0-2)	3 (1-9)
Wetlands	21 / 38	65.5	1.4 (0-3)	1 (0-6)	0 (0-1)	2.5 (1-8)
Broad-leaved forests	3 / 68	100.0	1.3 (1-2)	0 (0-0)	0 (0-0)	1.3 (1-2)
Coniferous forests	5 / 77	100.0	1.4 (1-2)	0 (0-0)	0.2 (0-1)	1.6 (1-2)

To test H5, we fitted three separate phylogenetic least squares models (PGLS), for area of occupancy, habitat range, and invaded climatic niche breadth. We fitted Pagel's lambda optimized through maximum likelihood, using the 'phylolm' package (Tung Ho & Ané, 2014). We log-transformed the response variables to improve normality (for invaded climatic niche breadth, we avoided zeros by adding the smallest non-zero value prior to transformation). We obtained a phylogenetic tree of the non-native plants in our dataset from the mega phylogeny of Jin & Qian (2019), built on those of Zanne et al. (2014) and Smith & Brown (2018). We used default settings (nodes = build.nodes.1, scenarios = "S3"). We fitted interactions between introduction pathways and: minimum residence time, native niche breadth, and plant height. We did not include interactions between pathways and categorical predictors, since we would have less than five observations for some combinations of factor levels. We did not include quadratic terms, because their addition did not improve models with a standardized linear term (95% confidence interval of quadratic terms overlapped zero, AICc increased, Table S2.4). Our full models for area of occupancy and habitat range fitted the data (likelihood ratio test, p-v < 0.05), and were not biased by multicollinearity (all variance inflation factors below five, 'performance' package; (Lüdecke et al., 2021). The full model of invaded climatic niche breadth did not fit the data (likelihood ratio test: p-v > 0.05), but the simpler models included in the "best" subset according to AICc did fit the data. We assessed patterns of covariation among plant traits, with particular interest on covariation with introduction pathways.

For H2-H5, we used multimodel inference to obtain model-averaged coefficients (full averaging: models without a variable shrank the coefficient of that variable towards zero). We fitted all combinations of explanatory variables, ranked the models using AICc, and kept for inference those models within six units of the best model (Harrison et al., 2018), using the ‘MuMIn’ package (Bartoń, 2023). Within that subset, we averaged two types of models separately: those not including interactions, and those including interactions. We compared the model-averaged coefficients between models without and with interactions. An interaction was considered as “significant” if the 95% confidence interval of the model-averaged coefficient did not overlap zero. Model selection tables were available in Appendix 2 (Table S2.5). We used the ‘emmeans’ package (Lenth, 2023) to calculate estimated marginal means and trends from the model of proportion of plants introduced through gardening in relationship to environmental variables defining the invaded niche.

All statistical analyses were performed in R-Studio (version 4.2.0; R Core Team, 2022).

3.4. Results

H1: Temporal trends in the contribution of pathways to the regional non-native flora

The total number of introduced plants increased five-fold over the past millennium (before 1500-2019, Fig. 2). The relative contribution of pathways to the regional pool of non-native plants changed substantially through time (Chi-square test: $p < 0.001$; Cramér’s V = 0.332). Plants with economic use (gardening, agriculture, and forestry) were the major contributors to the non-native flora across time periods. However, agriculture/forestry and gardening showed opposite temporal trends. Agriculture and forestry decreased five-fold (from 50% before 1500, to around 10% in the 20th and 21st centuries), in parallel with a three-fold increase in the relative importance of gardening (20% before 1500, to 50% at the beginning in the 20th century, and up to 75% from 1985-2019). In contrast, the unintentional pathway fluctuated in relative importance without a clear temporal trend (ranging between 20-40%).

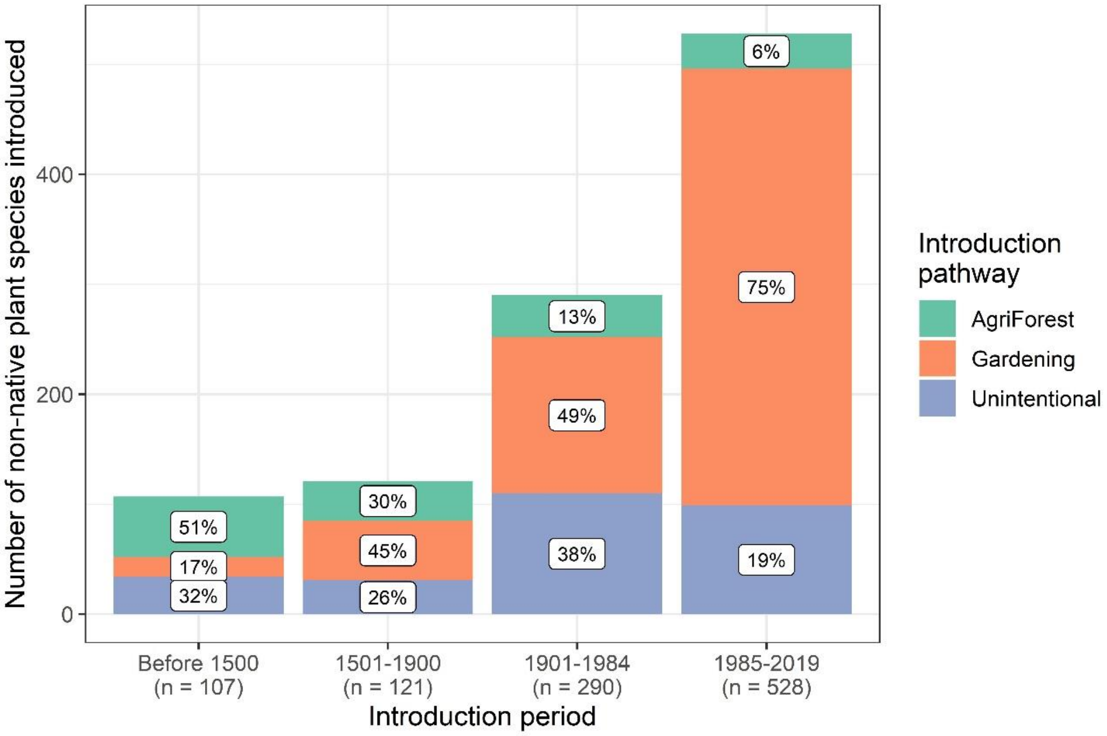

Fig. 3.2. Count of non-native plants per introduction period, with the relative importance of introduction pathways expressed as a percentage for each introduction period. N = 1046 (1025 non-native plants, 21 duplicated since they were introduced through two pathways). See Table S2.2 (Appendix 2) for contingency table. Abbreviations: AgriForest = agriculture and forestry.

H2-H4: Pathway-specific differences in the invaded niche

Introduction pathways influenced small differences in the invaded niche, mainly in habitat type, and secondarily in elevation (Fig. 3.3, Table S2.6). We concluded this with binomial GLMs, which related the proportion of non-native plants introduced through gardening to environmental variables (full model without interactions: McFadden's pseudo-R^2 = 0.141, AICc = 379.07). Across the three habitat types (cropland, urban, natural), gardening plants tended to be a minority of invaders, or have equal prevalence than unintentionally introduced plants (all three estimated marginal means ≤ 50% of invaders in a plot were introduced through gardening; model-averaged without interactions, Fig. 3.3). Urban and cropland habitats reduced invasion by gardening plants in favour of unintentionally introduced ones (on average, 34% vs 18%; Tukey pairwise contrast: p-v = 0.06). In contrast, natural habitats promoted invasion by gardening plants over unintentionally introduced ones: on average, gardening plants were 50% of invaders in natural habitats, which was a 60% increase and almost a three-fold increase compared to urban and cropland habitats (respectively, Tukey pairwise contrasts: p-v < 0.05). Furthermore, the positive effect of natural habitats on invasion by gardening plants was strongest in wetlands, riparian and coastal habitats (between 54-65% of invaders were introduced through gardening, between 16-32 invaded plots; Table 3.3, Fig. S2.3). Other pathway-specific differences regarding natural habitats could be unreliable due to small sample size (between 1-5 invaded plots, Table 3.3): gardening plants were the only invaders of broad-leaved and coniferous forests, they were absent in rock outcrops, and were a minority of invaders in scrublands and meadows (Appendix 2 Supplementary discussion). The invasion by non-native plants introduced by agriculture was overwhelmingly rare (Table 3.3), and was slightly promoted by riparian habitats (13% of all invaders, on average, Appendix 2 Supplementary discussion). Pathway-specific differences in the invaded niche related to elevation were small, and showed that high elevations favoured invasion by gardening plants compared to unintentional ones: for each increase in elevation of 236 meters (one standard deviation), the proportion of gardening plants in a plot increased by 0.06 (estimated marginal trend, Fig. 3.3).

Moreover, our results on pathway-specific differences in the invaded niche were largely unaffected by interactions between environmental variables (full model with interactions: McFadden's pseudo-R^2 = 0.152, AICc = 384.30). Interactions between environmental variables, per se, did not influence differences between pathways in the invaded niche (Fig. 3.3). Furthermore, the pathway-specific differences related to habitat type were unaffected by interactions. Elevation was unrelated to pathway-specific niche differences when interactions were modelled (this variable was significant but of secondary importance in models without interactions). Therefore, interactions further strengthened the result of substantial similarity in the invaded niche of plants introduced through different pathways.

H5: Pathway-specific differences in invasion success

Introduction pathways did not influence differences in invasion success (full models without interactions, Fig. 3.4, Table S2.7), measured through: area of occupancy (R^2_{adj} = 0.173, AICc = 219.97, Pagel's lambda = 0), habitat range (R^2_{adj} = 0.108, AICc = 158.48, Pagel's lambda = 0), and invaded climatic niche breadth (R^2_{adj} = 0.045, AICc = 268.29, Pagel's lambda = 0). In contrast, minimum residence time had a positive effect on invasion success: for each additional 62 years (one standard deviation), non-native plants increased in area of occupancy by 35 %, increased habitat range by 19 %, and increased invaded climatic niche breadth by 45 % (exponent of standardized model-averaged coefficients, Fig. 3.4, Table S2.7). The rest of plant attributes were largely unimportant.

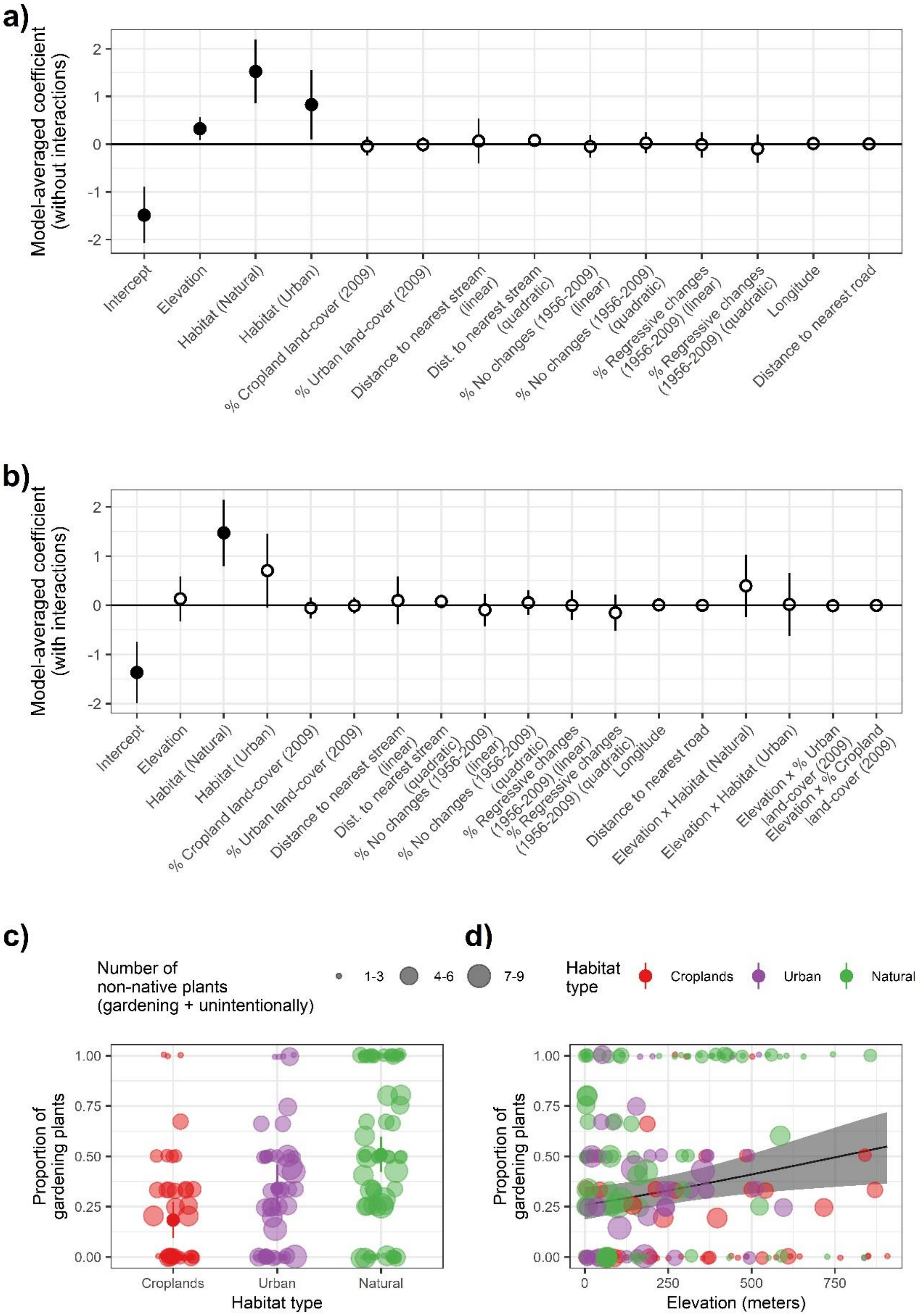

Fig. 3.3. Drivers of the proportion of gardening plants, in invaded plots in the Barcelona province. a) Model-averaged coefficients for models without interactions (estimates and 95% confidence intervals). b) Model-averaged coefficients for models with interactions (estimates and 95% confidence intervals). Estimates with a 95% confidence interval that includes zero have white filling. The intercept is the average proportion of gardening plants in plots located in cropland habitats, when all numerical predictors are at their mean value. Numerical predictors were

standardized. Coefficients were at the logit-scale. c) Estimated marginal means (estimate and 95% confidence interval, model-averaged from models without interactions). d) Predicted trend of elevation on the proportion of gardening plants, model-averaged from models without interactions (slope and 95% confidence interval). Dots represent the proportion of gardening plants per plot. N = 190 invaded plots. See Table S2.6 for the exact values of coefficients.

Moreover, our results on the effect of pathways on invasion success were mostly unchanged by interactions between pathway and non-native plant attributes (full models with interactions): area of occupancy (R^2_{adj} = 0.218, AICc = 227.22, Pagel’s lambda = 0), habitat range (R^2_{adj} = 0.132, AICc = 168.03, Pagel’s lambda = 0.502), and invaded climatic niche breadth (R^2_{adj} = 0.046, AICc = 279.93, Pagel’s lambda = 0). Interactions between pathways and traits, per se, did not affect invasion success. However, minimum residence time was unrelated to invasion success when interactions were modelled, except for the positive effect on invaded climatic niche breadth. Overall, the modelling of interactions reinforced the result that minimum residence time was a key driver of invasion success, while introduction pathways and other plant attributes were largely unimportant (Fig. 3.4). Plant attributes were correlated (Table S2.8, Fig. S3.4, and Appendix 2 Supplementary discussion). Unintentionally introduced plants were mostly annuals (60%: 18 out of 30), while gardening plants were mostly perennial herbs and shrubs or trees (43% and 47%, respectively: 18 and 20 out of 42), and agriculture and forestry plants were mostly shrubs or trees (67%: 6 out of 9). Therefore, unintentionally introduced plants were shorter than plants introduced through other pathways (around five meter difference with gardening plants, and around ten meter difference with agriculture and forestry ones, on average). Unintentionally introduced plants tended to have wider native niches compared to gardening plants (0.22 standard deviation difference, on average).

3.5. Discussion

Our study found evidence that introduction pathways of non-native plants changed in importance over the past millennium (1500-2019) with gardening replacing agriculture as the main pathway responsible for new introductions, while unintentional introductions were relatively constant over time. We also found that introduction pathways can shape the invaded niche, as observed in the studied area where natural habitats and high elevations were more likely to be invaded by gardening plants compared to unintentionally introduced ones. Moreover, invasion success was neither affected by introduction pathways, nor by interactions between pathways and plant attributes.

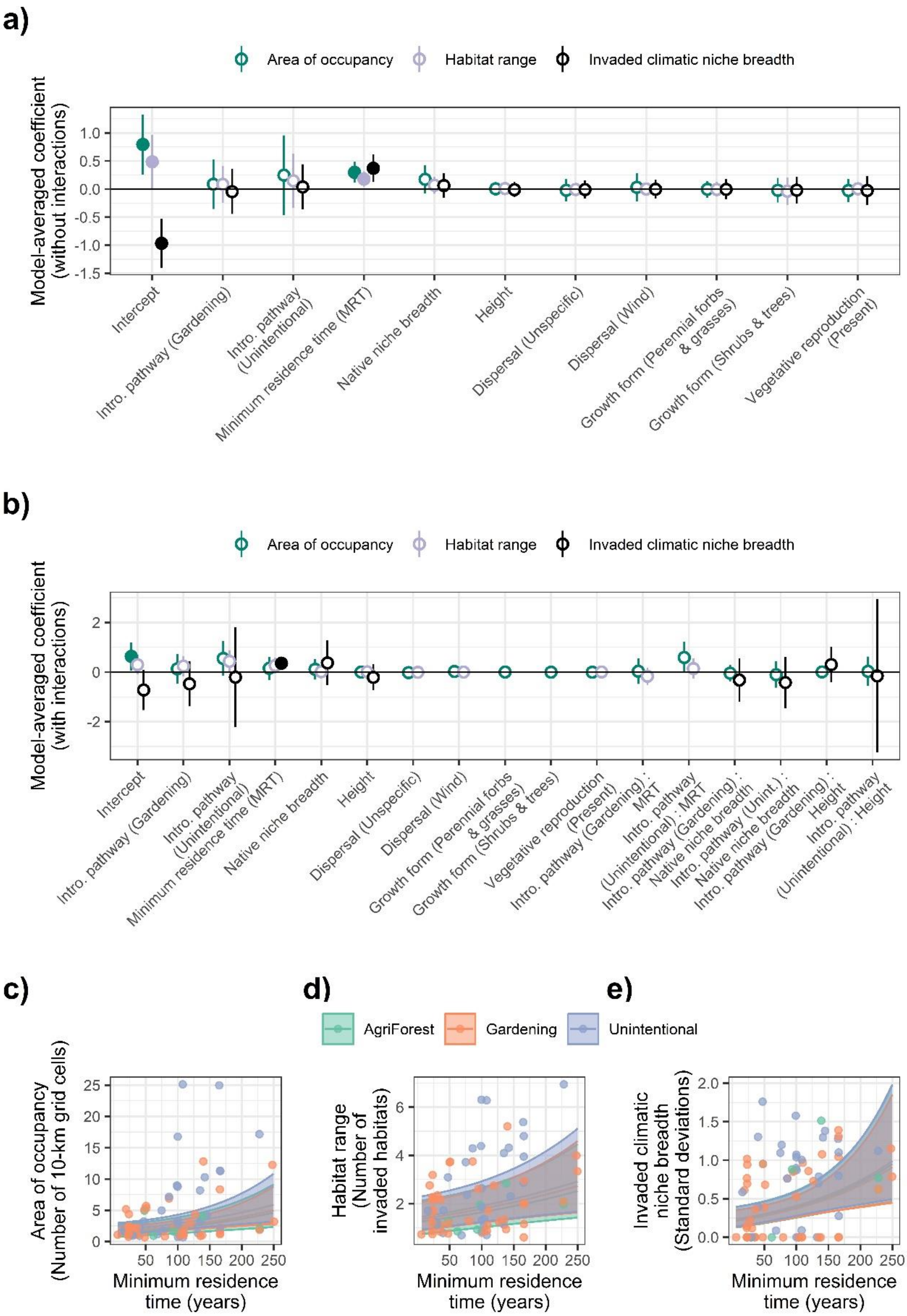

Fig. 3.4. Drivers of area of occupancy, habitat range, and invaded climatic niche breadth, in the Barcelona province. a) Model-averaged coefficients for models without interactions (estimates and 95% confidence intervals). b) Model-averaged coefficients for models with interactions (estimates and 95% confidence intervals). Estimates with a 95% confidence interval that includes zero have white filling. The intercept is the average area of occupancy, habitat range, or invaded climatic niche breadth, for non-native plants with introduction pathway as agriculture or forestry,

dispersal syndrome anemochorous, life form as annual forb or grass, and vegetative reproduction absent, when all numerical predictors are at their mean value. All response variables were log-transformed, and numerical predictors were standardized. c), d) e) Predicted trends of minimum residence time of invasion success for the different pathways, with 95% confidence intervals. Dots represented non-native plants. N = 81 (77 non-native plants, four duplicated since they were introduced through two pathways). See Table S2.7 for the exact values of coefficients. Abbreviations: AgriForest = agriculture and forestry, Intro. pathway = Introduction pathway, MRT = minimum residence time, Unint. = unintentional

Temporal trends in pathway importance

As hypothesised, over the past millennium (before 1500-2019), gardening replaced agriculture as the main introduction pathway contributing new plants of non-native flora. Such replacement could be related to the intensification of agriculture and the increase in urban population (Başnou et al., 2013; Ibàñez & Buriel, 2010). In other words, the use of plants has shifted from providers of food (dominance of agriculture before 1500), to providers of beauty (dominance of gardening after 1500; Dehnen-Schmutz, 2004; Pyšek et al., 2003). The total number of introduced plants increased five-fold, likely related to increased global trade, gardening activities, and research effort (Pyšek et al., 2011; Seebens et al., 2022).

Unlike agricultural introductions, unintentional introductions did not decrease in importance. This is surprising as many unintentionally introduced plants are transported through agricultural and farming activities, as contaminants of crop seed and forage (Kowarik & von der Lippe, 2007). Therefore, the different temporal trends between agricultural and unintentional introductions suggest that unintentionally introduced plants have increasingly relied on gardening, global trade or tourism (Cerrato et al., 2023; Sanz-Elorza, Mateo, et al., 2009). For example, seeds can contaminate gardening flower mixtures and container-grown ornamentals (Conn et al., 2008; Cossu et al., 2020; Ni & Hulme, 2021); seeds can also be transported on tourist's clothing and luggage, or onto containers carrying commodities (Ansong & Pickering, 2014; Harrower et al., 2018; Lucardi et al., 2020; Verloove et al., 2020). Notably, urban areas tend to concentrate gardening activities, tourism, and traded commodities (Early et al., 2016; Llurdés et al., 2009; Riera et al., 2021). This suggests that unintentionally introduced plants have diversified and spatially expanded their introduction epicentres over time: from being introduced mostly in cropland areas, to being introduced both in cropland areas and in urban areas.

Introduction pathways and the invaded niche

Introduction pathways were related to differences in the invaded niche, primarily in terms of habitat type. Contrary to our expectations (González-Moreno et al., 2013; Riera et al., 2021), plants introduced via gardening were not favoured over unintentionally introduced ones by urban land use (neither measured as habitat type nor as land-cover). Instead, few gardening plants were favoured by urban and cropland land uses, probably due to three non-exclusive explanations. First, urban land use would concentrate introduction epicentres both for gardening and unintentionally introduced plants due to a combination of gardening, trade and tourism activities (Ansong & Pickering, 2014; Cossu et al., 2020; Ni & Hulme, 2021; Riera et al., 2021). Second, gardening plants could be less pre-adapted to anthropogenic disturbance than unintentionally introduced ones, due to a lower incidence of the ruderal adaptive strategy (K. Guo et al., 2022; Lambdon et al., 2008a). Third, gardening plants could benefit less from dispersal by vehicles in urban environments than unintentionally introduced plants, because they tend to be taller and to have heavier seeds (von der Lippe & Kowarik, 2012; Yang et al., 2021).

In contrast, gardening plants were most invaders in some natural habitats: riparian, coastal and wetland habitats. This difference could relate to habitat-specific patterns in propagule pressure. Most propagules reaching riparian and wetland habitats could be from gardening plants, since urban areas are commonly located along waterways (Kühn et al., 2017), and urban areas concentrate gardening activities (Padayachee et al., 2017; Riera et al., 2021). Similarly, coastal habitats could receive a majority of non-native propagules from gardening plants, due to the popular use of perennial succulents for xeriscaping (Sanz-Elorza et al., 2004a). While pathway-specific niche differences could also relate to differences in vegetation structure and composition across habitats, we lacked data on native vegetation to provide additional insights (Clotet et al., 2016).

Contrary to our expectation, gardening plants became slightly more prevalent with increasing elevation than unintentionally introduced ones, agreeing with previous work (Chytrý et al., 2021; Thuiller et al., 2006). Gardening plants could invade high elevations due to human care: irrigation and protection from frost could allow gardening plants to send propagules into habitats surrounding gardens, even in the harsh environmental conditions that characterize high elevations (Mack, 2000). In contrast, other studies have found that intentionally introduced plants became more scarce with increasing elevation (Akatova & Akatov, 2019; McDougall et al., 2011), suggesting regional differences linked to different socioeconomic context.

Interactions between elevation and selected environmental variables did not determine pathway-specific differences in the invaded niche, contrary to our hypothesis. In addition, pathways did not influence differences in topography including road proximity, nor historical landscape across the ten studied habitat types. This was contrary to previous work in our study area on forest edges and coastal habitat patches (Başnou et al., 2015; González-Moreno et al., 2013), suggesting that pathway-specific niche differences do not necessarily generalize from particular habitats to a wider range of environments.

Introduction pathways and invasion success

Introduction pathways did not affect the invasion success of non-native plants. Rather, invasion success was affected by minimum residence time, without relevant interactions between minimum residence time and introduction pathways, contrary to our last hypothesis, and to previous work on area of occupancy in our study area (Riera et al., 2021). Our findings agree with studies that found no effect of pathways on area occupancy (Harris et al., 2007; Küster et al., 2008; Speek et al., 2011); nor on a metric that aggregated area of occupancy, climatic niche breadth and abundance (Carboni et al., 2016). These results suggest that economic use is not necessarily linked to the potential invasion success of the non-native plants. In fact, unintentionally introduced plants can have certain traits that help them to become invaders, compensating for the lack of human care associated with their introductions. These could include dispersal-related traits (von der Lippe & Kowarik, 2012), wider native climatic niches, ruderal strategy (K. Guo et al., 2022; Lambdon et al., 2008a), or human factors such as a diversification of introduction epicentres.

In contrast to our results, other studies have found an effect of pathways on invasion success. Most studies on area of occupancy reported greater area for intentionally introduced plants (Akasaka et al., 2012; Egawa et al., 2019; W. Guo et al., 2019; Pyšek et al., 2015), while we previously found the reverse pattern in our study area (Riera et al., 2021). Other works found that gardening plants reached the highest habitat range among intentionally introduced plants (Rojas-Sandoval & Ackerman, 2021), while pathway-specific differences in niche breadth depended on which environmental variables defined the niche (Thuiller et al., 2012). Moreover, some works indicate that invasion status can vary the effect of introduction pathways on both area of occupancy and habitat range (K. Guo et al., 2022; Pyšek et al., 2011). Overall, the disparity of results suggests that the relationship between introduction pathways and invasion success could depend on the ecological and socioeconomic context of the study area, and also on methodological choices (e.g. how invasion success was measured, level of detail in the pathway classification).

Minimum residence time had a positive effect on invasion success, in agreement with previous studies on area of occupancy (Akasaka et al., 2012; Casado et al., 2018; Gassó et al., 2009; Harris et al., 2007; Riera et al., 2021; Speek et al., 2011; Wilson et al., 2007), habitat range (Essl et al., 2009; Fristoe et al., 2021; Lazzaro et al., 2020; Pyšek et al., 2011), and invaded climatic niche breadth (Banerjee et al., 2021). The positive effect of minimum residence time on area of occupancy and niche breadth suggests that non-native plants have diversified their niches over time, a process that was correlated with geographical spread over time. This expansion over time resulted in similar area of occupancy and niche breadth across pathways, and in pathway-specific nuances in the type of invaded environmental conditions.

The key role of minimum residence time on invasion success probably relates to time as a proxy of many potentially relevant processes that modulate the species' invasion success, which are not mutually exclusive. For example, residence time of an introduced species could include the effects of the change of the main introduction pathway over time: the longer a species was introduced, the more likely it is affected by the diversification and spatial expansion of introduction epicentres. Residence time could also be a proxy of accumulative propagule pressure: human activity has spread the propagules of old introductions for a longer time, compared to recent ones (Gassó et al., 2009). Further, residence time could be a proxy for the opportunity to evolve local adaptation (Colautti & Barrett, 2013; Oduor et al., 2016) and adaptive phenotypic plasticity (Parker et al., 2003; Ross et al., 2009).

Our results suggest that management strategies should attempt to track socioeconomic changes (Bradley et al., 2012). In particular, developing economies could monitor the market of ornamental plants, while taking into account that an increase in global trade, tourism and gardening could lead to a steady influx of unintentionally-introduced plants (Cerrato et al., 2023). Our study corroborates the substantial importance of residence time on the success of non-native plants, and the importance of early and preventive management. The finding of similar invasion success between gardening and unintentional introductions, suggests that preventive management should have a broad scope, such as monitoring the market of ornamental plants and placing biosecurity measures (Bayón & Vilà, 2019; Edney-Browne et al., 2018; Hulme et al., 2008). Our results on pathway-specific differences in the invaded niche also suggest that preventing gardening introductions could be most beneficial to prevent invasion of natural habitats and high elevations, while preventing unintentional introductions could be most beneficial to prevent invasion of urban and cropland habitats.

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Chapter 4

Introduction pathways affect niche breadth and niche harshness of non-native plants in their invaded range

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4.1. Abstract

The invasion success of non-native plants depends on their ability to overcome environmental filters that impede their survival, reproduction and dispersal. Knowledge of introduction pathways (how species are introduced) provides a great opportunity for preventive management, yet the relationship between pathways and overcoming environmental filters remains unclear. Here, we test how introduction pathways (intentional, unintentional or both) affect the invaded realized niche breadth (i.e., breadth of invaded environmental conditions) and niche harshness (i.e. stress level of invaded environmental conditions) of 220 non-native plants recorded in nearly 76,000 vegetation plots across Europe. We show that a combined introduction by both intentional and unintentional pathways, a broad niche in the native range, and a long residence time in the invaded range lead to a broad invaded niche of non-native plants. Regarding niche harshness, intentional pathways were associated with the invasion of dry habitats, whereas unintentional pathways were linked to the invasion of saline and high-elevation habitats. We suggest that preventive management should focus on reducing trade with ornamental plants that arrive by multiple pathways and have a broad native climatic niche, as well as on implementing more stringent biosecurity measures.

4.2. Introduction

The successful invasion by non-native plants requires overcoming geographical and environmental filters: plants are first transported into a recipient area, where they vary in their ability to survive, reproduce and disperse under a set of environmental conditions (Blackburn et al., 2011). A key factor in overcoming the geographical filter are introduction pathways: processes that transport non-native plants, such as gardening and global trade (Harrower et al., 2018; Hulme et al., 2008). Plants with a common introduction pathway tend to share biological attributes, such as growth form or dispersal-related traits (K. Guo et al., 2022; W. Guo et al., 2019; Lambdon et al., 2008a; von der Lippe & Kowarik, 2012). Pathways also summarize features of the introduction process that are difficult to measure, such as propagule pressure (Pergl et al., 2017; Donaldson et al., 2014) and spatial location of introduction epicentres (Donaldson et al., 2014; Ni & Hulme, 2021; Riera et al., 2021). Despite their potential importance, it remains unclear whether different introduction pathways affect how non-native plants overcome environmental filters. Therefore, a detailed understanding of the role of pathways is central to invasion ecology and effective management strategies, including the prevention of new introductions (Hulme et al., 2008; McGeoch et al., 2016).

The link between introduction pathways and overcoming environmental filters might be investigated by addressing two aspects of the plant's invaded realized niche (the set of invaded environmental conditions; Fristoe et al., 2021; Riera et al., 2024). The first is niche breadth, which relates to the invasion under a wide range of environmental conditions (Ainsworth & Drake, 2020; Fristoe et al., 2021). The second is niche harshness, which relates to the invasion of stressful environments (Alexander et al., 2016; Alpert et al., 2000; Zefferman et al., 2015). Previous tests relating introduction pathways to environmental filters have used a limited set of environmental variables, either approximating niche breadth through a single perspective (habitats, Rojas-Sandoval & Ackerman, 2021; Pyšek et al., 2011); or climate, (Thuiller et al., 2012; Banerjee et al., 2021; but see Riera et al., 2024), or addressing niche harshness considering a single type of stressful conditions (elevation gradients; Akatova & Akatov, 2019; Chytrý et al., 2021; Thuiller et al., 2006; McDougall et al., 2011; Riera et al., 2024). Moreover, these studies related pathways to niche breadth and niche harshness mainly at the national or sub-national scale (Akatova & Akatov, 2019; Banerjee et al., 2021; Chytrý et al., 2021; Pyšek et al., 2011; Riera et al., 2024; Thuiller et al., 2006, 2012; but see McDougall et al., 2011; Rojas-Sandoval & Ackerman, 2021). Thus, we still need to evaluate the invaded niche of non-native plants at a broader geographical scale while integrating different environmental variables.

Here, we fill this gap by testing how introduction pathways affect the ability of non-native plants' to overcome these environmental filters on the European continent. We integrate multiple aspects of niche breadth (Fristoe et al., 2021; Riera et al., 2024; Zelený & Chytrý, 2019), and major stressful environmental variables that limit plants' establishment and spread (Alpert et al., 2000; Zefferman et al., 2015). First, we asked whether the types of introduction pathways are associated with the niche breadth of non-native plants. Second, we asked whether the type of introduction pathway is associated with the invasion of harsh environmental conditions by non-native plants (niche harshness).

We gathered data on the presence of 220 non-native plants in nearly 76,000 georeferenced vegetation plots across Europe (from the European Vegetation Archive; (Chytrý et al., 2016). For the first question, we quantified niche breadth by using complementary metrics (based on habitats, climate and co-occurring flora) and modelled the effect of introduction pathways (intentional, unintentional, or both), using phylogenetic generalized least square models, while accounting for key species' characteristics (native climatic niche breadth, growth form, dispersal syndrome, height, residence time). For the second question, we quantified the contribution of intentional introduction pathways to the invasion of each plot, and modelled the effect of environmental harshness (drought, salinity, oligotrophy, and elevation), by using generalized linear mixed-effect models, while accounting for land-cover (urban and cropland) and habitat type.

4.3. Methods

Data

We gathered presence data of 220 non-native vascular plants and co-occurring flora in 75,957 georeferenced vegetation plots across Europe. To do so, we extracted 1,237,259 vegetation plots from the European Vegetation Archive (EVA; Chytrý et al., 2016, accessed February 2021, Fig. S3.1; Table S3.1). Then, vegetation plots were classified into habitat types of the hierarchical habitat classification of the European Nature Information System (EUNIS; Chytrý et al., 2020). The classification was performed to three hierarchical levels: level three (166 types) > level two (46 types) > level one (eight types). For example, a given vegetation plot could be classified as the habitat "Temperate *Salix* and *Populus* riparian forest" (level three), which is a type of "Broadleaved deciduous forests" (level two), which is itself a type of "Forests and other wooded land" (level one). The habitat classification was performed using a computer-based expert system based on attributes such as species composition and geographical position (Chytrý et al., 2020). We then reduced bias due to uneven sampling effort, by performing geographical resampling (Knollová et al., 2005): we overlaid a grid with cell size of 1.25' x 0.75' longitude x latitude (around 1.5 x 1.4 km) on the georeferenced plots and randomly kept a maximum of three plots for each combination of grid cell and habitat, using JUICE version 7.1 (Tichý, 2002). We filtered the resulting 793,093 plots by removing those classified to inland surface waters (thus increasing homogeneity of the dataset) and those that could not be classified unambiguously to a unique habitat. Furthermore, we kept only the plots with presence of at least one terrestrial neophyte, i.e. plants of extra-European origin introduced after 1500 AD to our study area (based on expert knowledge of the author team, and the Euro+Med database, http://ww2.bgbm.org/EuroPlusMed/). The final database included 75,957 plots (Fig. S3.1), with median area = 50 m^2 (range: 1–1000 m^2) and median year of collection = 1997 (range: 1914–2020). Of those plots, 81% (N = 61,579 plots) could be classified to the maximum level of detail in the hierarchy (level three), while the remaining 19% could only be classified to coarse habitat types (level one).

Assessment of niche breadth

To address our first question (how pathways were associated with the niche breadth of non-native plants), we calculated five complementary metrics of niche breadth in the invaded range for each species: (i-iii) habitat range (at the three hierarchical levels of the EUNIS habitat classification system), (iv) biotic niche breadth, and (v) climatic niche breadth. Habitat range was a proxy of the breadth of vegetation types invaded by the species. We calculated it as the count of the different invaded habitats at three levels of the EUNIS hierarchy. The resulting variables were highly correlated to habitat range at level 1, so we focus on level 1 in the main text and show the results with levels 2 and 3 in Figs. S3.2-S3.5 and Tables S3.2-S3.4. Biotic niche breadth was a proxy of the degree of habitat specialization, based on co-occurrences with native and non-native plants in the plots where the species was recorded (Zelený & Chytrý, 2019). An habitat generalist would have high beta diversity among plots since it co-occurs with a broad set of plants (the opposite being true for specialists). We calculated it by averaging Whittaker's multiplicative beta (Zelený & Chytrý, 2019) across ten randomly drawn samples (ten plots per random sample, with replacement; 'genspe' package, Zelený, 2015). Before calculation, we removed outliers (plots with a very different species composition), following published guidelines (Botta-Dukát, 2012). The resulting units were the mean number of invaded communities with no overlap in species composition. Climatic niche breadth was a proxy of the breadth of climatic conditions across plots invaded by the species. We calculated it through the geometric mean of the standard deviation of the first five axes of a Principal Component Analysis (PCA) of a set of bioclimatic variables with low correlation (following Palma et al., 2021; Appendix 3 Supplementary methods). We extracted bioclimatic variables from CHELSA (Karger et al., 2017) using ArcGIS 10.7.

For each non-native plant species (Table 4.1), we gathered data on the introduction pathway and a series of potential drivers of niche breadth (Ainsworth & Drake, 2020; Banerjee et al., 2021; Fristoe et al., 2021; Giulio et al., 2021; Lazzaro et al., 2020; Palma et al., 2021; Thuiller et al., 2012): climatic niche breadth in the native range, dispersal syndrome, growth form and height, while also accounting for minimum residence time (Banerjee et al., 2021; Fristoe et al., 2021; Lazzaro et al., 2020; Pyšek et al., 2011). Introduction pathway in Europe was based on published databases (Chytrý et al., 2021; Klotz et al., 2002; Riera et al., 2021) and expert knowledge of the author team, complemented with literature review (if no data was available). Gathering pathway information from a broad range of sources was necessary to account for the fact that non-native plants can be introduced through more than one pathway (Harrower et al., 2018). Therefore, we coded the pathway in three complementary ways: (i) three mutually exclusive categories (intentional, unintentional, both); (ii) intentionality proportion (number of assignments of the intentional pathway / total number of pathway assignments), (iii) two non-exclusive categories (intentional, unintentional; duplicating 62 non-native plants introduced through both pathways). Thus, we could account for pathway diversity (i) and pathway identity (ii-iii). For instance, *Erigeron canadensis* was assigned the unintentional pathway 11 times, and the intentional pathway three times (out of 13 independent sources). This species was coded in separate models as follows: (i) the "both" pathway, (ii) an intentionality proportion of: 3/(3+11) = 0.214, and (iii) the "intentional" and "unintentional" pathway (the species was duplicated). Native climatic niche breadth was a proxy of the breadth of climatic conditions endured by non-native plants in their native range, following the same methodology used to calculate the climatic niche breadth in the invaded range. We obtained occurrence data in the native range by overlying occurrence coordinates on polygons delimiting the native range of each non-native plant (‘sf’ package; Pebesma, 2018a). We downloaded occurrence coordinates from the Global Biodiversity Information Facility (GBIF; Chamberlain et al., 2022; GBIF, 2022), and filtered the occurrences following published guidelines (Feng et al., 2019; Zizka et al., 2019; Appendix 3 Supplementary methods). The native range was taken from the Plants of the World Online webpage (http://www.plantsoftheworldonline.org/), and the polygons delimiting such native range were level 2 regions of the Taxonomic Database Working Group (Brummitt, 2001). Dispersal syndrome was set as the main mechanism that dispersed seeds away from the parental plant: anemochorous, endozoochorous, epizoochorous, unspecific; it was inferred based on the external morphology of the diaspore if not stated in databases (Chytrý et al., 2021; Sanz-Elorza et al., 2004a). Growth form included both longevity and growth habit: annual herbaceous, perennial herbaceous, shrub/tree, taken from published databases (Chytrý et al., 2021; Sanz-Elorza et al., 2004a). Height was the mean height of the plant reported in floras (in meters; Chytrý et al., 2021; Pignatti et al., 2017–2019). Minimum Residence Time (MRT) was calculated as the difference between 2022 and the year of first record in nature. The earliest year was taken from published databases (Chytrý et al., 2016, 2021; Klotz et al., 2002; Riera et al., 2021; Seebens, 2020; Seebens et al., 2018), complemented by literature review when no data was available in those databases.

Assessment of niche harshness

To address the second question (how pathways are associated with niche harshness of non-native plants), we quantified the proportional importance of the intentional pathway to the invasion of each plot by calculating the arithmetic mean of the intentionality proportion of all non-native plant species in each plot. For example, in a plot containing *Robinia pseudoacacia* (intentionality proportion = 1) and *Erigeron canadensis* (intentionality proportion = 0.214), the intentional pathway would have a proportional importance of: (1 + 0.214)/2 = 0.607. A direct pairwise combination in the environmental conditions invaded by non-native plant species introduced through each pathway was not advisable because a single plot may be invaded by many non-native plants, each introduced through a different pathway combination. Therefore, a pairwise comparison would include a substantial number of duplicates, reducing the quality of the test.

We gathered data for each plot on environmental harshness, approximated through drought, salinity, oligotrophy, and elevation (Table 4.2). We used this broad selection of variables to model the multiple types of environmental harshness, which is known to reduce the presence of non-native plants (Alexander et al., 2016; Alpert et al., 2000; Zefferman et al., 2015). Salinity, drought and oligotrophy were binary variables recording whether each type of stress occurred in the level three habitat type that each plot was classified to (based on expert knowledge; Table S3.5). Elevation was available for each plot as EVA database data (Chytrý et al., 2020). We also gathered data on potential confounding variables, including proxies of anthropogenic disturbance: urban land-cover, cropland land-cover, habitat type, annual precipitation, longitude, latitude and country. Annual mean temperature and annual precipitation were extracted from CHELSA

(Karger et al., 2017). Urban and cropland land-cover (proportion of each class in a 500 m buffer, excluding the ocean) were extracted from the CORINE dataset. Habitat type was the level one habitat of the EUNIS classification (eight types). Longitude, latitude and country in which the plot was located were available as EVA database data (Chytrý et al., 2020). We extracted climatic and land-cover data with ArcGIS v10.7. We used only the subset of plots classified to level three in the EUNIS habitat classification (N = 61,579 plots), since the detailed identity of each invaded habitat was necessary to calculate metrics of harshness that consider local conditions (salinity, drought, and oligotrophy). An overview of the distribution of non-native plants across harsh conditions and habitats in Europe is provided in Table S3.6.

Statistical analyses

To address our first question, we tested the effect of introduction pathway, plant characteristics (native climatic niche breadth, dispersal syndrome, growth form, height), and minimum residence time on niche breadth, by fitting phylogenetic least square models (Pagel's lambda optimized through maximum likelihood, 'phylolm' package; (Tung Ho & Ané, 2014). We built a phylogenetic tree for all non-native plants in our data set, using the 'V.PhyloMaker' package (Jin & Qian, 2019), with default settings (nodes = build.nodes.1, scenarios = "S3"); and bounded absent genera to a closely related genus.

We fitted a separate model for each of the five metrics of niche breadth and for each of the three categorizations of the introduction pathway (N = 15 models, Table S3.2). Since the three categorizations reached similar results, we report only the model with pathway as three exclusive categories (intentional, unintentional, both) in the main text. The remaining models are summarized in Figs. S3.2-3.4 and Tables S3.2-3.4. To improve model fit, we ln- transformed the three metrics of habitat range. Our models were not biased by collinearity (all variance inflation factors (VIFs) in all full models < 5, Table S3.2). To assess the association among metrics of niche breadth, we calculated a Pearson's correlation matrix. Furthermore, since introduction pathways covary with characteristics that can be linked to invasion success (K. Guo et al., 2022; W. Guo et al., 2019), we explored patterns of covariation among introduction pathways, plant traits and minimum residence time.

To address our second question, we tested the effect of environmental harshness on the proportional contribution of the intentional pathway to the invasion of each plot, by fitting a generalized linear mixed model (GLMM, 'glmmTMB' package; Brooks et al., 2017). The GLMM had binomial distribution (logit link), and country as random intercepts (to account for country-specific differences in trading history and in the recording of non-native plants in vegetation plots). We removed annual mean temperature (VIF = 12) to reduce collinearity (all VIFs in the reduced model < 5). We obtained marginal and conditional R^2 values with the 'MuMIn' package (theoretical variances method; Bartoń, 2022). Spatial autocorrelation was low in the model's residuals (assessed following Padullés Cubino et al., 2021; see Fig. S3.6).

Table 4.1. Variables used to relate niche breadth to non-native plant characteristics in our statistical models, split by response and explanatory variables. Abbreviations: CV = Coefficient of variation (standard deviation / mean), EUNIS = European Nature Information System. Values are provided with a dataset in which non-native plants introduced through both intentional and unintentional pathways were not duplicated (N = 220 non-native plants).

Variable	Description and summary
Response variables: niche breadth	
Habitat range	Count of invaded habitats, at three levels of the EUNIS habitat classification system. We presented results for level 1 (range = 1–8, median = 4, CV = 0.46) in the main text, levels 2 (range = 1–24, median = 6, CV = 0.67) and 3 (range = 2–113, median = 10, CV = 0.97) yielded similar conclusions (see Appendix 3). Unit = habitat.
Biotic niche breadth	Degree of habitat specialization (range = 2.24–7.93, median = 5.81, CV = 0.18). Unit = mean number of communities with no overlap in species composition.
Climatic niche breadth	Breadth of invaded climatic conditions, in ordination space (range = 0–1.53, mean = 0.83, CV = 0.37). Unit = standard deviations.
Explanatory variables: non-native plant attributes	
Introduction pathway	Process that transported and introduced non-native plants to our study area (N = 3, both = 62, only intentional = 105, only unintentional = 53). Alternative coding yielded similar results (see Appendix 3): two categories (intentional = 167, unintentional = 115), and intentionality proportion (range = 0–1, median = 0.88, CV = 0.71, unitless).
Minimum residence time	Number of years since the first record outside of cultivation in our study area (range = 36–472, mediab = 162, CV = 0.54). Unit: years.
Native climatic niche breadth	Breadth of climatic conditions inhabited in the native range, in ordination space (range = 0.134–1.829, median = 0.956, CV = 0.27). Unit = standard deviations.
Height	Mean height reported in floras (range = 0.03–47.5, median = 0.82, CV = 2.02). Unit = meter.
Dispersal syndrome	Main mechanism that disperses the seed away from the parental plant (N = 4: anemochorous = 46, endozoochorous = 40, epizoochorous = 17, unspecific = 117).
Growth form	Combination of longevity and growth habit (N = 3: annual herbaceous = 73, perennial herbaceous = 77, shrub/tree = 70).

Table 4.2. Variables used to relate niche harshness to introduction pathways in our statistical models, split by response variable, explanatory variables describing multiple aspects of niche harshness, explanatory variables describing potential confounders, and random effects. Abbreviations: CV = Coefficient of variation (standard deviation / mean), EUNIS = European Nature Information System. N = 61,579 plots.

Variable	Description and summary
Response variable	
Mean intentionality proportion	Proportional importance of the intentional pathway to the invasion of each plot (range = 0.00–1.00, median = 0.36, CV = 0.77): arithmetic mean of the intentionality proportion of all non-native plants in each plot. For example, a plot containing *Robinia pseudoacacia* (intentionality proportion = 1) and *Erigeron canadensis* (intentionality proportion = 0.214), would have mean intentionality proportion = (1 + 0.214) / 2 = 0.607. Unit = unitless.
Explanatory variables: niche harshness	
Elevation	Vertical distance between plot and sea level (range = -7–2,720, median = 166, CV = 0.99). Unit = meter.
Annual mean temperature	Yearly average of temperature (range = -1.7–19.7, median = 10, CV = 0.25). Unit = ºC.
Salinity	Occurrence of stress due to presence of salt in the soil, or sea-spray, in the level 3 habitat type to which the plot was classified (N = 2: no = 60,842, yes = 737).
Drought	Occurrence of stress due to scarcity of moisture in the soil (at least seasonally), in the level 3 habitat type to which the plot was classified (N = 2: no = 51,353, yes = 10,226).
Oligotrophy	Occurrence of stress due scarcity of nutrients, in the level 3 habitat type to which the plot was classified (N = 2: no = 53,592, yes = 7,987).
Explanatory variables: potential confounders	
Urban land-cover	Proportion of urban land-cover in a 500 m buffer around the plot, excluding the ocean (range = 0.00–1.00, median = 0, CV = 1.55). Unit = unitless.
Cropland land-cover	Proportion of cropland land-cover in 500 m buffer around the plot, excluding the ocean (range = 0.00–1.00, median = 0.43, CV = 0.79). Unit = unitless
Habitat type	Type of habitat that the plot was classified to, at level 1 of the EUNIS habitat classification system (N = 8: coastal = 1,635, forest = 18,076, grasslands = 11,030, heathlands, scrub and tundra = 2,004, little soil, sparse vegetation = 153, littoral biogenic = 308, man-made = 25,387, wetlands = 2,986).
Annual precipitation	Yearly sum of rainfall (range = 203–2,730, median = 691, CV = 0.31). Unit = millimetre.
Longitude	Coordinate specifying the east-west position of the plot (range = -10.26–30.46, median = 14.47, CV = 0.58). Unit = degree.
Latitude	Coordinate specifying the north-south position of the plot (range = 34.93–68.35, median = 49.19, CV = 0.08). Unit = degree.
Random effect	
Country	Country in which the plot was located (N = 37).

Prior to all analyses, we standardized all numerical explanatory variables to a mean of zero and unit variance (Schielzeth, 2010). We then fitted quadratic terms, if they improved the AICc (Akaike Information Criterion corrected for small sample sizes) of a univariate model containing a linear term, and the 95% confidence interval of the quadratic term did not overlap zero. For all analyses, we used multimodel inference to obtain model-averaged coefficients (full-averaging; 'MuMIn' package, Bartoń, 2022). We ranked models using AICc, and kept for inference the subset within six units of the top-ranked model. We approximated the relative importance of predictors through standardized general dominance: the proportional contribution of each predictor to the model's total explained variation (dominance analysis, 'domir' package, Luchman, 2023). For the models of niche harshness, we used estimated marginal means and trends to calculate effects at the proportion scale (Lenth, 2023). We performed all analyses with R version 4.2.0 (R Core Team, 2022).

4.1. Results

Introduction pathways versus niche breadth and niche harshness

Introduction pathway was a significant driver of habitat range (number of invaded habitats, R^2_{adj} of Phylogenetic Generalized Least Squares models, PGLS = 0.25), one of our metrics of niche breadth for non-native plant species introduced to Europe (Fig. 4.1; Fig. S3.2-S3.3). Non-native plants introduced to Europe both intentionally and unintentionally were present in one more habitat than plants introduced only unintentionally (e.g. contaminants of commodities, hitchhikers on vessels), but were similar to those introduced only intentionally (e.g. gardening, forestry). Introduction pathways were not significantly related to biotic niche breadth (number of invaded communities with no overlap in species composition; R^2_{adj} = 0.06) and climatic niche breadth (breadth of invaded climatic conditions; R^2_{adj} = 0.13). Overall, introduction pathways were the second or third most important correlate of niche breadth (relative importance: 16-26%; Fig. S3.3, Table S3.4).

Introduction pathways were associated with niche harshness (Generalized Linear Mixed Model, GLMM, country as random intercepts, $R^2_{marginal}$ = 0.311, $R^2_{conditional}$ = 0.350; Fig. 4.2, Fig. S3.7, Tables S3.7-S3.8). Dry conditions promoted invasion through intentional pathways (i.e. greater proportional contribution of intentional pathways to the invasion in dry vs. non-dry plots, model-averaged estimated marginal means ± standard error: 0.433 ± 0.022 vs 0.369 ± 0.020), while oligotrophy had no effect. Saline conditions and increasing elevation were associated with reduced invasion through intentional pathways (non-saline vs. saline plots: 0.509 ± 0.022 vs. 0.293 ± 0.027; 100 m vs 2500 m above sea level: 0.398 ± 0.026 vs. 0.243 ± 0.075). Niche harshness was a comparatively small part of the correlation between introduction pathways and the invaded environmental conditions (relative importance: 5%; Fig. S3.7; Table S3.7).

Introduction pathways vs other drivers of niche breadth

Non-native plants with high minimum residence time (i.e. introduced a long time ago) had greater habitat range and biotic niche breadth but similar climatic niche breadth than recent introductions (relative importance in PGLS: 64%, 47% and 6%, respectively, Fig. 4.1; Fig. S3.2-S3.3; Tables S3.3-S3.4). Climatic niche breadth in the native range had a positive effect on climatic niche breadth in the invaded range, but was unrelated to biotic niche breadth and habitat range (relative importance: 66%, 33% and 4%, respectively). Dispersal syndrome, plant height, and growth form, were of minor importance to niche breadth (each had a relative importance < 10%, and non-significant effects).

Plants introduced both intentionally and unintentionally were mostly annual and perennial herbs and arrived earlier than those introduced through only one of the pathways. Plants introduced only unintentionally were mostly annual herbs (none were shrubs or trees) and comprised most of epizoochorous plants. Plants introduced by both pathways and those introduced only unintentionally were shorter and had broader native climatic niches than plants introduced only intentionally (Figs. S3.8-S3.9; Table S3.9).

Introduction pathways vs other niche characteristics

In addition to niche breadth and niche harshness, the type of introduction pathway correlated with additional niche variables (Fig. 4.2; Fig. S3.7, Tables S3.7-S3.8). Habitat type was strongly correlated to pathway-specific differences (relative importance in a GLMM: 83%): invasion by intentional pathways was lowest in man-made habitats and highest in forests (four-fold difference). Increasing cropland land-cover was associated with reduced invasion by intentional pathways (relative importance: 5%). Urban land-cover, annual precipitation, longitude and latitude were of minor importance to pathway-specific differences in the invaded niche (each had relative importance < 5%; see Supplementary results and Supplementary discussion).

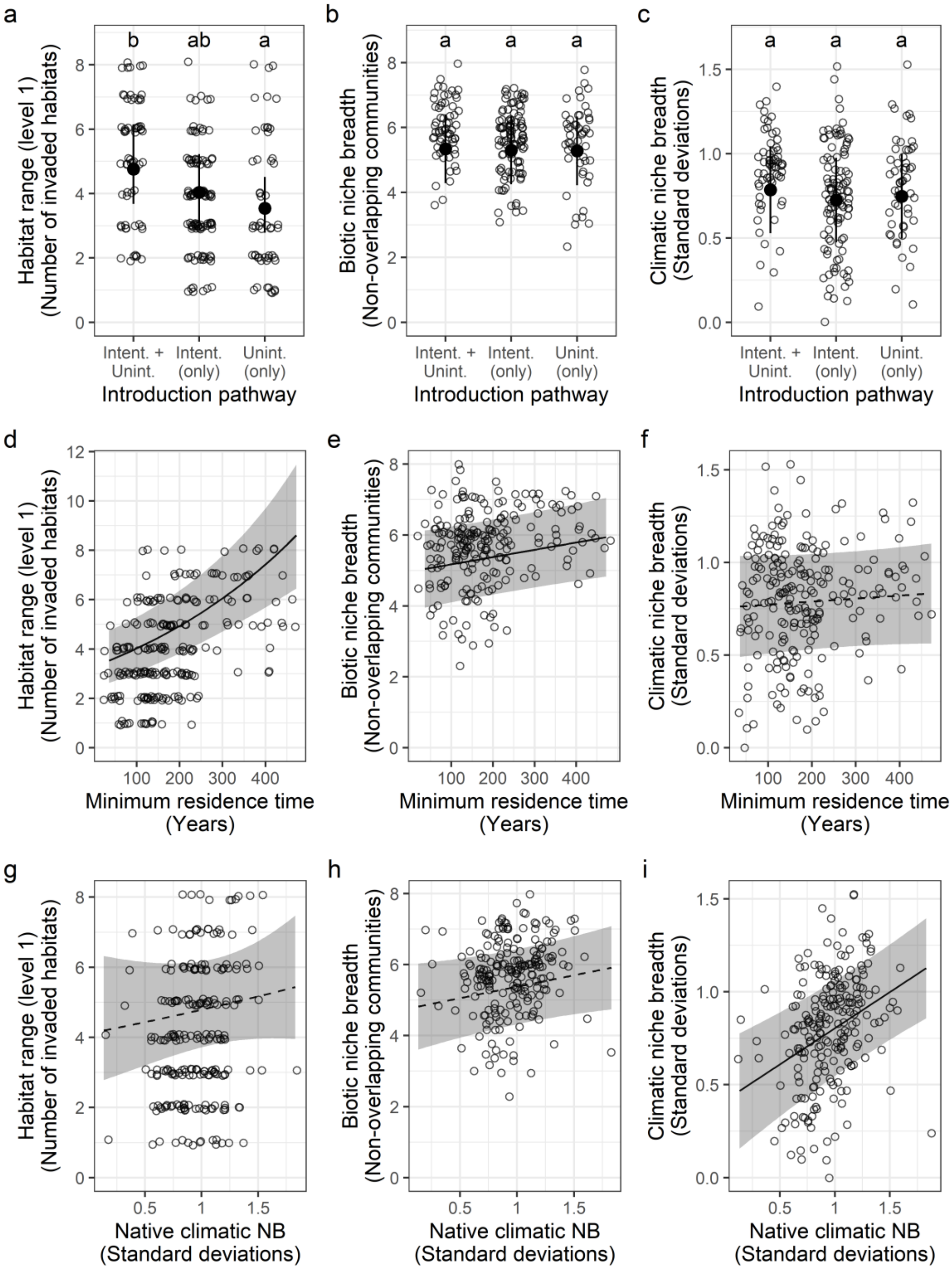

Fig. 4.1. Effects of introduction pathways, minimum residence time, and native climatic niche breadth, on niche breadth of non-native plants across Europe. Model-averaged predicted means (a-c) and trends (d-i, dashed lines indicate non-significant slopes), with 95% confidence intervals. Dots show non-native plants. Note that habitat range predictions were back-transformed from the log scale. N = 220 for the habitat range and climatic niche breadth models (b-c, e-f, h-i), N = 215 for the biotic niche breadth (a, d, g). Alternative coding of introduction pathways as two categories (intentional, unintentional) or intentionality proportion yielded similar results (Fig. S3.3). See Appendix 3 Table S3.2 for the coefficients. Abbreviations: Intent. = Intentional, NB = Niche breadth, Unint. = Unintentional.

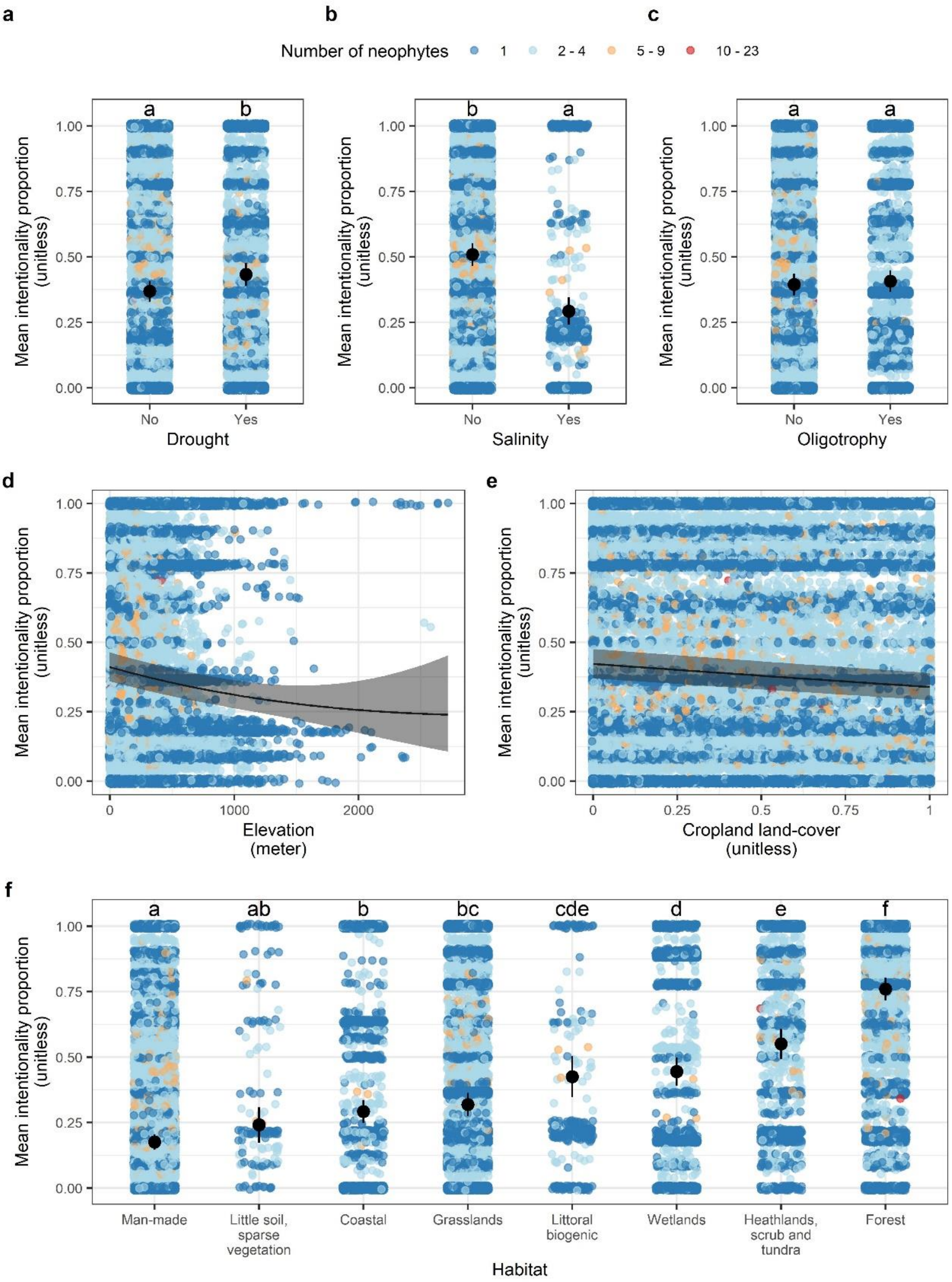

Fig. 4.2. Effects of niche harshness, and additional niche variables, on mean intentionality proportion (how much intentional pathways contributed to the invader pool of a vegetation plot). Model-averaged estimated marginal means (a-c, f) and trends (d-e), with 95% confidence intervals. Different letters above means indicate statistically significant pairwise differences (Tukey contrast). Dots show invaded plots, with random noise added for visualization (N = 61,579). See Appendix 3 Table 3.5 for exact values.

4.2. Discussion

Our study shows that the type of introduction pathway affected both niche breadth and niche harshness. Therefore, we provide evidence that in addition to triggering invasions by overcoming geographical filters, introduction pathways also shape the success of non-native plants at overcoming environmental filters.

A combination of intentional and unintentional introduction was associated with a broader niche in the invaded range, in terms of the number of invaded habitats, than only unintentional introduction. We suggest that the advantage of combined introduction pathways could relate to high propagule pressure (high number of seeds reaching target habitats; Pergl et al., 2017) due to the diversification of the sources of propagules. High propagule pressure would reduce the chance of population extinction or loss of genetic variation (Uller & Leimu, 2011). In turn, this would allow a greater probability of evolution of local adaptation (Oduor et al., 2016) and adaptive phenotypic plasticity (Richards et al., 2006), two mechanisms that could allow a plant to overcome many environmental filters in the invaded range. Moreover, plants introduced through both pathways would start these adaptive processes at a greater diversity of spatial locations (Pergl et al., 2017), because the introduction epicentres of intentional and unintentional pathways often do not overlap (Riera et al., 2021). Intentional introductions take place mostly in urban areas, due to the concentration of public and private gardens (Riera et al., 2024). Unintentional introductions would also concentrate in urban areas, which are the final destination of contaminated commodities and ornamentals (Hulme et al., 2008; Ni & Hulme, 2021); but also in croplands (sowing of contaminated seeds; Harrower et al., 2018), and trade and touristic infrastructures (harbours and airports where people and commodities carry hitchhiking seeds; Ni & Hulme, 2021).

The advantage of plants with a combined intentional and unintentional introduction at overcoming environmental filters could also be related to covariation with minimum residence time and niche breadth in the native range (Pergl et al., 2017). First, we found that plants introduced through both pathways tended to be introduced earlier. The increase in niche breadth over time (Ainsworth & Drake, 2020; Banerjee et al., 2021; Fristoe et al., 2021; Lazzaro et al., 2020; Pyšek et al., 2011) could reflect that plants need time to disperse to different areas with different environmental conditions (i.e. exert propagule pressure), and thereby occupy a broader niche (Ainsworth & Drake, 2020; Banerjee et al., 2021). Furthermore, time is necessary for evolutionary processes that facilitate invasion of a wide breadth of conditions (Banerjee et al., 2021; Richards et al., 2006; but see Oduor et al., 2016). Second, we found that non-native plants introduced by both pathways tended to have broader niches in their native range. The greater niche breadth in the invaded range for plants with a broader niche in the native range suggests the importance of pre-adaptation to inhabiting a wide breadth of environmental conditions (W. Guo et al., 2019). Moreover, species with a broad native climatic niche could also benefit from increased propagule pressure, as they are more likely to be transported accidentally (because they may be more geographically widespread; W. Guo et al., 2019) and cultivated more frequently (because the broad tolerance is a desirable trait; W. Guo et al., 2019).

Whether non-native plants were introduced intentionally or unintentionally was largely unrelated to niche breadth in the invaded range, similarly to previous work on habitat range and climatic niche breadth in an invaded range in North-East Spain (Riera et al., 2024). We suspect that plants introduced through a single pathway share disadvantages compared to plants with both intentional and unintentional introduction. Those would be, in particular, a lower propagule pressure, lower diversity of introduction epicentres (see above), shorter residence time, and narrower native climatic niche breadth. Previous studies at smaller spatial extents found that pathway-specific differences in niche breadth depended on which environmental variables defined the niche (Thuiller et al., 2012), or on the invasion status of non-native plants (Pyšek et al., 2011). Overall, the varying relationship between introduction pathways and niche breadth in the invaded range suggests that economic use is not necessarily linked to a successful invasion (Riera et al., 2024).

We showed that the type of introduction pathways was associated with the overcoming of harsh environmental filters, depending on the type of stress: intentional pathways were associated with the invasion of dry habitats, while unintentional pathways were associated with both saline and high-elevation habitats. Previous results have linked the invasion of high-elevation habitats to both intentional (Chytrý et al., 2021; Riera et al., 2024; Thuiller et al., 2006); and unintentional pathways (Akatova & Akatov, 2019; McDougall et al., 2011). This possibly reflects heterogeneity across mountain regions (Alexander et al., 2011; McDougall et al., 2011), and variation in the proportion of intentionally introduced plants across regions worldwide (van Kleunen et al., 2020).

The success of unintentional pathways in overcoming harsh filters related to elevation and salinity could be related to the effects of specific traits. First, unintentionally introduced plants have a higher incidence of short stature (Riera et al., 2024), epizoochorous dispersal, and light seeds (von der Lippe & Kowarik, 2012), which are traits associated with human mobility (dispersal on clothing and vehicles; Ansong & Pickering, 2014; von der Lippe & Kowarik, 2012; Yang et al., 2021). Human mobility would promote the invasion of harsh sites, which are usually remote, by increasing propagule pressure (Alpert et al., 2000; Zefferman et al., 2015). Second, unintentionally introduced plants have a high prevalence of annual growth form (Pyšek et al., 2011; Riera et al., 2024) and ruderal strategy (K. Guo et al., 2022; Lambdon et al., 2008a), i.e. traits associated with anthropogenic disturbance. The anthropogenic disturbance would make high-elevation and saline areas more vulnerable to invasion by increasing propagule pressure, ameliorating stress, and creating vegetation gaps (Alpert et al., 2000; Kalusová et al., 2023; Zefferman et al., 2015). The advantage of the ruderal strategy at invading harsh conditions is supported by previous work documenting that most invaders in alpine habitats are ruderals (Alexander et al., 2016). Our finding of positive associations of invasion by unintentional pathways with cropland land-cover and man-made habitats (Riera et al., 2024) supports that unintentionally introduced plants benefit disproportionately from anthropogenic disturbance.

Intentional pathways were only associated with overcoming harsh filters in the case of dry habitats, possibly because intentional pathways are more likely to introduce pre-adapted stress-tolerant plants (K. Guo et al., 2022; Lambdon et al., 2008a), such as succulents commonly used for xeriscaping (*Agave americana* and *Opuntia spp.*), which invade xeric habitats in the Mediterranean (Lambdon et al., 2008a). Other features of intentional introduction were probably insufficient to promote the invasion of harsh habitats. While intentionally introduced plants are often provided with human care (irrigation, protection from frost; (W. Guo et al., 2019; Pyšek et al., 2011), such protection is not provided to seedlings that establish outside of the cultivation area. Non-native plants have been sometimes intentionally released into dry conditions such as coastal dunes to stabilize the terrain or for ornament (*Acacia saligna* and *Rosa rugosa*; Guarino et al., 2021; Kalusová et al., 2023). However, we found that coastal habitats were mostly associated with unintentional pathways. Therefore, pre-adaptation to stress tolerance and deliberate release could be less effective to invade harsh conditions than the ability of unintentionally introduced plants to take advantage of anthropogenic disturbance and human mobility.

To sum up, our analysis reveals that introduction pathways, by affecting how non-native plants overcome environmental filters in their invaded range, represent an important factor in invasion success. Being introduced through a combination of intentional and unintentional pathways is associated with higher niche breadth in the invaded range, in combination with a long residence time and a broad niche in the native range. Intentional and unintentional pathways pushed non-native plants to invade different harsh habitats, with stress caused by drought, or salinity and elevation, respectively. These results have the potential to guide management strategies focusing on pathways. Preventive efforts could reduce the trade of non-native plants with multiple pathways or with a broad native climatic niche, in favour of plants representing lower risk (Hulme et al., 2008). Unintentional introduction could be prevented through more stringent biosecurity measures, as suggested by the successful impact of recent biosecurity protocols (Seebens et al., 2017).

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Chapter 5

Climatic niche conservatism in non-native plants is largely dependent on their climatic niche breadth in the native range

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5.1. Abstract

1. Confidence in predictions of non-native species' spread relies on the niche conservatism hypothesis, which poses that climatic niches are preserved over time and space. Because plants introduced through the same introduction pathway (gardening, agriculture, forestry, unintentional) tend to share some features of the introduction process and biological attributes, the extent of niche conservatism might be influenced by how and when species of particular attributes have been introduced.

2. We compared the realized climatic niches between the native (global) and invaded ranges (mainland Spain), through ordination and kernel smoothers. We calculated niche conservatism metrics (i.e. overlap, unfilling, stability, expansion, pioneering), for a set of 164 plant species. Niche conservatism metrics were then related to a plant's introduction pathway, minimum residence time, growth form, and native climatic niche breadth.

3. On average, niche stability accounted for 75% of niche occupancy, while around 62% of species showed some degree of niche shift. The climatic niche was most conserved for annual and perennial herbs, plants introduced a long time ago, and those with broad climatic niches in their native range. Introduction pathways had a non-significant effect. Niche conservatism metrics were neither explained by interactions of minimum residence time with introduction pathways nor with growth form. Native climatic niche breadth was the most important correlate of niche conservatism metrics.

4. Synthesis. Non-native plants largely occupy similar climatic conditions in their invaded and native range, supporting the niche conservatism hypothesis. This boosts confidence in predictive models of non-native plants' spread. This study highlights that niche conservatism is better explained by a plant's ability to cope with broad climatic conditions, rather than by its introduction history or growth form.

5.2. Introduction

The ecological niche, defined as the set of environmental conditions that allow population persistence for a particular species, is a key concept in ecology and conservation biology (Guisan et al., 2014). Importantly, the niche is the theoretical basis of Ecological Niche Models (ENMs), which predict the distribution of species by matching their occurrence to environmental conditions (Franklin, 2010; Guisan et al., 2014). The majority of ENMs approximate the realized niche through field observations, rather than the fundamental niche based on ecophysiological requirements (Guisan et al., 2014). ENMs are essential for effective conservation strategies (Guisan et al., 2014; Liu et al., 2020), including the management of invasive species, in order to prioritize resources to prevent and curb their spread in the areas identified as suitable by models (McGeoch et al., 2016). The pervasive negative effects of invasive species (Bacher et al., 2024), highlight the need for reliable prediction of their spread (Liu et al., 2022).

An important factor that boosts the reliability of predictions of non-native species' spread is niche conservatism (Liu et al., 2022): similar occupancy of environmental conditions in the invaded range compared to the native range (Pearman et al., 2008; Peterson, 2011). Most evidence concerning niche conservatism comes from non-native plants (Liu et al., 2020). While some studies have reported substantial conservatism (Liu et al., 2020; Petitpierre et al., 2012), some have found important niche shifts between ranges (Atwater et al., 2018; Early & Sax, 2014). Therefore, substantial interest lies in understanding the factors influencing the extent of niche conservatism.

A plant's introduction pathway (gardening, forestry, agriculture, unintentional; Hulme et al., 2008) can influence niche conservatism (Atwater et al., 2018; Liu et al., 2020). These effects are likely related to pathway-specific differences in human husbandry and climate matching in introduction epicentres (i.e. initial points of introduction and spread; Donaldson et al., 2014). For example, cultivation has been related to reduced niche conservatism compared to unintentional introductions (Atwater et al., 2018), possibly because cultivation increases the chance of population establishment (Gallagher et al., 2010). However, important variation might occur among intentionally introduced plants. Among *Acacia* species introduced to South Africa, niche overlap was highest for species introduced for forestry, possibly due to substantial climate matching to secure growth with minimal human husbandry (Donaldson et al., 2014). There have been few tests on the influence of pathways on niche conservatism (Atwater et al., 2018; Donaldson et al., 2014; Liu et al., 2020), and those comparing multiple types of intentional pathways are restricted to a single genus (Table S4.1; Donaldson et al., 2014). Thus, we still lack a general understanding of the differences in niche conservatism among plant species introduced for gardening, forestry and agriculture, which are main introduction pathways worldwide (Hulme et al., 2008). This is an important knowledge gap, given the crucial role of introduction pathways in the design of preventive management strategies in biological invasions (McGeoch et al., 2016).

Because introduction pathways of non-native plants have changed over time (Cerrato et al., 2023; Riera et al., 2024), we expect the effect of introduction pathways on niche conservatism to depend on minimum residence time (i.e. time since first record outside cultivation). Previous studies indicate that unintentional introductions have become partly decoupled from agricultural introductions (Cerrato et al., 2023; Riera et al., 2024; Sanz-Elorza, Mateo, et al., 2009), and are recently more closely related to trade and tourism (Ansong & Pickering, 2014; Lucardi et al., 2020). Importantly, agricultural weeds tend to experience high climate matching because they are pre-adapted to the same climate as the crops they infest, unlike introductions with trade and tourism (Neve et al., 2009; Peters et al., 2014). Therefore, increasing residence time would correlate to decreasing climate matching among unintentionally introduced plants. Previous studies on minimum residence time generally reported negative correlations with niche conservatism (Early & Sax, 2014; Liu et al., 2020), although some studies report no or a weak positive effect (Gallagher et al., 2010; Petitpierre et al., 2012; Sychrová et al., 2022). To the best of our knowledge, whether niche conservatism is influenced by an interaction between minimum residence time and introduction pathways has not been previously tested (Table S4.1).

Plants with a common pathway also tend to share some biological attributes: unintentionally introduced plants are more likely to be herbs (Atwater et al., 2018; Riera et al., 2024), and to have wider climatic niches in their native range, in comparison to gardening plants (Riera et al., 2024). Moreover, because herbaceous growth form and short height correlate to faster rates of molecular and niche evolution among plant lineages (Lanfear et al., 2013; Smith & Beaulieu, 2009), herbaceous non-native plants could be more likely to evolve changes in their fundamental niches than shrubs and trees. However, previous studies show less niche conservatism among shrubs and trees than among herbaceous plants (Atwater et al., 2018), no effect of growth form (Gallagher et al., 2010), or no effect of generation time (nor in interaction with minimum residence time; Early & Sax, 2014). Therefore, it remains unclear whether there is a consistent effect of growth form on niche conservatism. Likewise, plants with a wide climatic niche in the native range might have less climate space left to occupy, promoting the extent of niche conservatism (Dellinger et al., 2016; Early & Sax, 2014; Sychrová et al., 2022). It remains to be tested which is the simultaneous influence of introduction pathway, minimum residence time, growth form and climatic niche breadth in the native range on niche conservatism (Table S4.1).

In this study, we draw data on 164 plant species invading mainland Spain, to test whether niche conservatism is modulated by introduction pathways, growth form, native climatic niche breadth and minimum residence time; while accounting for potential interactions. Specifically, we expect: (1) reduced niche conservatism for intentionally introduced plants than for unintentionally introduced ones, particularly for gardening plants compared to species introduced by forestry (Atwater et al., 2018; Donaldson et al., 2014); (2) greater niche conservatism with increasing minimum residence time, particularly for unintentionally introduced plants; (3) reduced niche conservatism in annual and perennial herbs compared to shrubs and trees, particularly for annual herbs with greater minimum residence time (Early & Sax, 2014); and finally (4) greater niche conservatism among plants with wider niches in the native range (Dellinger et al., 2016; Early & Sax, 2014).

5.3. Methods

Plant occurrences in the native and invaded ranges

We used the non-native vascular flora of mainland Spain as a study-system because of its diverse environmental conditions: this area encompasses 12 climate types, from hot desert to subarctic (Instituto Geográfico Nacional, 2019). Furthermore, Spain has experienced temporal changes in pathway importance that allow to test our second expectation (Riera et al., 2024; Sanz-Elorza, Mateo, et al., 2009).

We compiled a list of naturalized neophytes in mainland Spain from Sanz-Elorza et al. (2004a). Naturalized neophytes are non-native plant species introduced to Spain after 1500, which form stable populations without human intervention. We harmonised the nomenclature using the Plants of the World Online website (POWO, 2021). We did not include in our analyses aquatic and parasitic species, and those without data on the year of first record (see "Explanatory variables of climatic niche conservatism" section), leading to a preliminary selection of 306 species.

We downloaded occurrence coordinates from the Global Biodiversity Information Facility (GBIF, 2021), using the 'rgbif' package (Chamberlain et al., 2021). We filtered the download relying on available metadata and the 'CoordinateCleaner' package (Zizka et al., 2019), with full details provided in the Supporting Information (Feng et al., 2019).

Polygons delimiting the native range (anywhere in the world) and invaded range in Spain were taken from the Taxonomic Database Working Group (Brummitt, 2001), using three nested scales: level 1 (continental) > level 2 (sub-continental to sub-national) > level 3 (national to sub-national).

The native range were level 2 regions taken from the Plants of the World Online webpage (POWO, 2021). A quality-check was performed by comparing level 2 regions against Germplasm Resource Information Network (GRIN, 2021), and by comparing level 1 regions against Sanz-Elorza et al. (2004a). Moreover, we kept some species considered by POWO as native to Spain, following the more updated checklist of the vascular flora of the Iberian Peninsula (Ramos-Gutiérrez et al., 2021). This led to the correction of 14% of the species in the final dataset (Table S2). The invaded range was the level 3 polygon delimiting mainland Spain.

We overlaid the filtered GBiF occurrence data, onto the polygons delimiting the native and invaded ranges ('sf' package; Pebesma, 2018b). We kept plants with at least 20 occurrences in both the native and invaded ranges, reducing our initial selection from 306 to 164 species.

Climatic niches

For each species we calculated its realized climatic niche (hereafter, "climatic niche"), by extracting 19 bioclimatic variables on the occurrences, at a resolution of 2.5 arc-minutes from WorldClim v1.4 (Hijmans et al., 2005), using the 'raster' package (Hijmans, 2021). We kept a single occurrence per pixel.

We used the relevant level 2 polygons for the native background climate (potentially different for each species), removing those polygons with no GBiF occurrences (2% of species; Table S3). All species had the same non-native background climate (mainland Spain).

Climatic niche conservatism

We decomposed the climatic niche through ordination and kernel density smoothing (PCA-env; Broennimann et al., 2012), which has become a gold standard to study climatic niche conservatism (Liu et al., 2020). This approach assesses climatic niche conservatism in reduced environmental space (PCA-env; Broennimann et al., 2012), while accounting for differences in availability of climatic conditions and sampling effort (Broennimann et al., 2012; Guisan et al., 2014).

For each species separately, we calibrated a Principal Component Analysis (PCA) on the 19 bioclimatic variables of the native and the invaded range. We used the scores of the first two PCA axes to create a two-dimensional climatic space, which we divided into a 100x100 grid (Guisan et al., 2014). We calculated smoothed occupancy of climatic conditions using the PCA scores for the climates and occurrences in both ranges (‘ecospat’ package; Di Cola et al., 2017).

We used the resulting smoothed occupancies of climatic conditions across the native and invaded ranges, to calculate representative metrics of climatic niche conservatism; because climatic niches have multiple ways of being dissimilar (Guisan et al., 2014; Liu et al., 2020). We used metrics of climatic niche conservatism that accounted for climatic conditions present in both the native and invaded range (analog conditions), and for climatic conditions exclusive to one of them (non-analog conditions), for two reasons. First, occupancy of non-analog conditions could affect the accuracy of predictive models (Carlin et al., 2023). Second, given the diversity of climates on Earth, the occupancy of non-analogue climatic conditions may be important an important niche component (Atwater et al., 2018; Carlin et al., 2023).

We calculated five components of climatic niche conservatism between the native and the invaded range: niche overlap, unfilling, stability, expansion and pioneering (Fig. 5.1). Niche overlap was calculated as Schoener’s D, which is the overlap in niche occupancy between the native and the invaded range, expressed as a proportion (0 = no overlap, 1 = complete overlap). To calculate niche overlap, we did not correct occurrence densities by the density of available climate in either range, since previous authors have linked such a correction to artefacts (Datta et al., 2019). The remaining components divided the whole niche occupancy (native and invaded range; Fig. 5.1) into: unfilling (occupancy of climatic conditions available in both ranges, but only occupied in the native one), stability (occupancy of climatic conditions available and occupied in both ranges), expansion (occupancy of climatic conditions available in both ranges, but only occupied in the invaded one), and finally, pioneering (occupancy of climatic conditions available only in the invaded range). For illustrative purposes, we also calculated abandonment (occupancy of climatic conditions available only in the native range), which did not influence conclusions on the correlates of niche conservatism (Fig. S4.1). We used the ‘ecospat’ package (Di Cola et al., 2017), and functions kindly provided by Dr. Blaise Petitpierre (https://github.com/ecospat/ecospat/issues/65).

To assess how removal of marginal climates affected conclusions, we used climatic conditions up to the 100th, the 90th and the 75th quantiles (Guisan et al., 2014; Hill et al., 2017). Changes in coefficients’ significance were very rare (Fig. S4.2). Therefore, we present results with the 75th quantile, since they would be the least influenced by marginal climates.

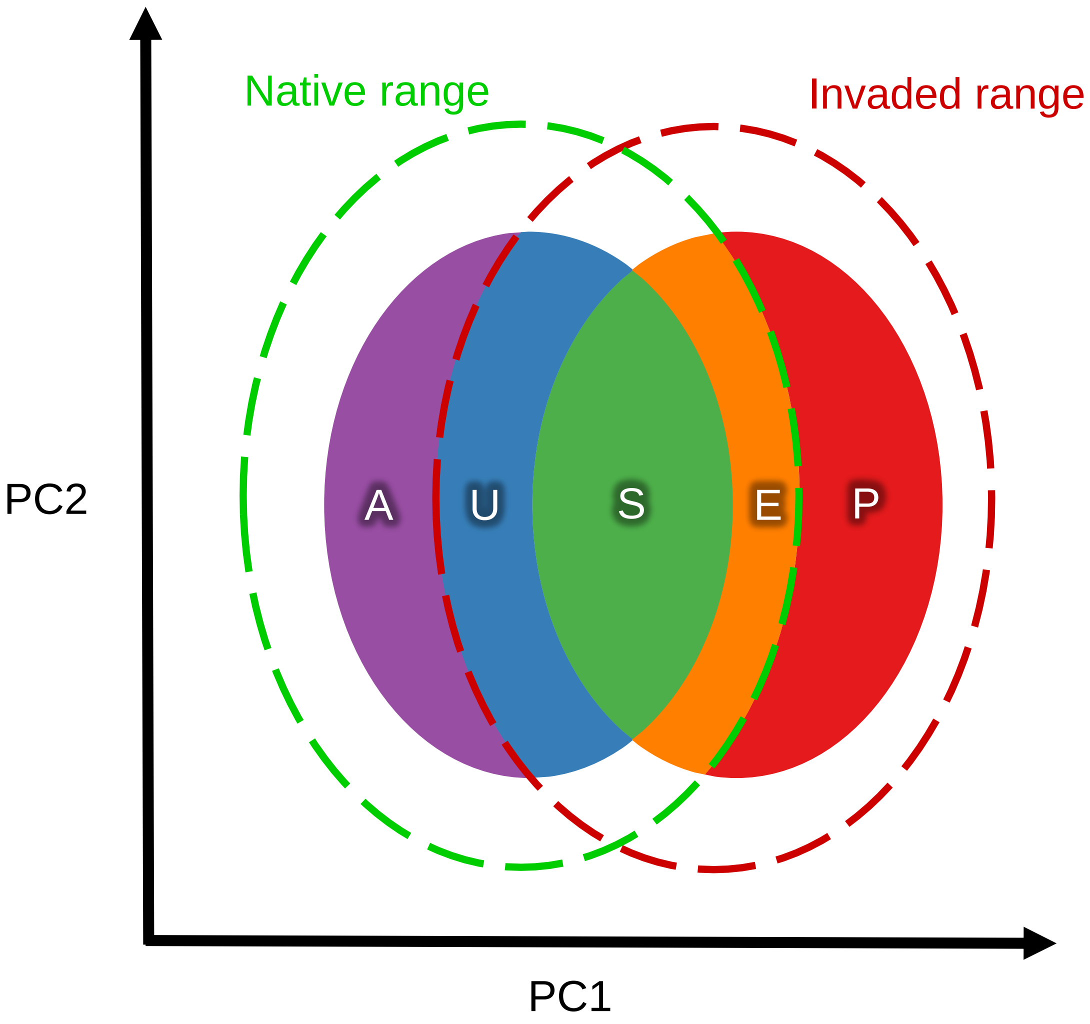

Fig. 5.1. Diagram of the climatic niche conservatism components between the native and the invaded ranges of non-native plants in two Principal Components (PC) ordination axes. Available climatic conditions are shown with dashed lines (green for the native range, red for the invaded range). Occupied climatic conditions are shown with solid colours, with labels: A = Abandonment, U = Unfilling, S = Stability, E = Expansion, P = Pioneering. Abandonment and Pioneering involve non-analog climatic conditions (available only in either the native or the invaded range), while Unfilling, Stability and Expansion involve analog climatic conditions (present in both the native and invaded ranges). The abandonment component was omitted in the model presented in the main text, we further note that modelling abandonment did not influence conclusions (Fig. S4.1). This diagram was based on previous works (Atwater et al., 2018; Guisan et al., 2014).

To assess the overall level of niche conservatism, we calculated the percentage of non-native plants in which stability accounted for more than half of niche occupancy (Liu et al., 2020). Furthermore, to facilitate comparisons with previous studies, we calculated the percentage of species that had values of unfilling, expansion or pioneering > 10%, which has been used as a partly arbitrary threshold indicating relevant low levels of niche conservatism (Dellinger et al., 2016; Hill et al., 2017; Petitpierre et al., 2012). We did not consider niche overlap as an unequivocal indicator of a niche conservatism on its own, because it could be influenced by niche abandonment (Fig. S4.3).

Explanatory variables of climatic niche conservatism

For each of the 164 plant species we gathered data on their introduction pathway, minimum residence time, growth form, and climatic niche breadth in their native range. The final sample size was 175 because 11 plant species were introduced through two different pathways, and were thus duplicated in the dataset.

The introduction pathway categories were gardening (N = 89), agriculture (N = 6, including plants introduced for livestock consumption), forestry (N = 6) and unintentional (N = 74); and were taken from published databases (Aymerich & Sáez, 2019a; Sanz-Elorza et al., 2004a).

Minimum residence time was the difference between 2021 and the year of first record outside cultivation, from the First Record Database v2.0 (Seebens, 2021; Seebens et al., 2018). In case a species was not included in this database, it was consulted in other sources (Anthos, 2021; J. A. Campos & Herrera, 2009; Riera et al., 2021; Romero, 2007; Sanz-Elorza et al., 2008, 2011; Sanz-Elorza, González, et al., 2009).

Growth form accounted for longevity and growth habit, and we used the categories: annual herb (N = 48), perennial herb (N = 73), shrub or tree (N = 54). We classified prostrated succulents as perennial herbs, and arborescent succulents as shrub or tree. We took growth form from Sanz-Elorza et al. (2004a).

Native climatic niche breadth was obtained by calculating a PCA with the climatic values of the native occurrences (19 bioclimatic variables), and aggregating the standard deviation of the scores of the first five axes with the geometric mean (Palma et al., 2021).

Unintentionally introduced plants were disproportionately more likely to be annual herbs and less likely to be shrubs or trees, compared to gardening and forestry plants (Fig. S4.4 and Table S4.4). Unintentionally introduced plants also had the widest climatic niches in their native range, although this covariation was weaker. Forestry introductions were the most recent, while agricultural introductions were the oldest.

Statistical analyses

We modelled the effect of introduction pathways, minimum residence time, growth form and native climatic niche breadth on niche overlap by fitting a mixed-effects beta regression, with fixed precision and a logit link ('glmmTMB' package; Brooks et al., 2017). We chose the beta regression because it is suitable for continuous proportions that do not arise from counts (Douma & Weedon, 2019). We accounted for phylogenetic relatedness by fitting random intercepts (genus nested within family, taken from: Sanz-Elorza et al. (2004a). We note that the variance component of taxonomic family was very close to zero (singular fit), but we chose to keep it because the phylogenetic non-independence is part of our study design. We quantified explained variation through the marginal and conditional R^2, which are, respectively, the variation explained by the fixed effects, and by the fixed and random effects ('MuMIn' package; Bartoń, 2023).

We modelled the effect of introduction pathways, minimum residence time, growth form and native climatic niche breadth on the other four climatic niche conservatism components (unfilling, stability, expansion and pioneering) by fitting a Dirichlet regression, which is a suitable method to model continuous proportions which are split among more than two categories (Douma & Weedon, 2019). We implemented the "alternative" parametrization, which modelled (i) the four expected proportions under the constraint that they must sum up to one (unfilling was the base category with coefficients = 0; multinomial logit link), and (ii) precision (density around expected proportions; log link; Fig. S4.2 and Table S4.5). We transformed the raw proportions to prevent exact zeroes and ensure the five proportions summed up to one ('DirichletReg' package; (Maier, 2021). We accounted for phylogenetic relatedness by including phylogenetic covariates: ordination axes representing phylogenetic relationships, obtained from a principal coordinate analysis on a matrix of phylogenetic distances (Desdevises et al., 2003; Jin & Qian, 2019). We quantified explained variation with a pseudo-R^2: we calculated the squared Spearman's correlation between the fitted values and the transformed proportions, and calculated the mean across the four components.

Our modelling strategy followed four steps. We first (1) built models without interactions: mixed-effects beta regression for niche overlap, and Dirichlet regression for the remaining climatic niche conservatism components. We scaled continuous explanatory variables to: mean = 0, standard deviation = 1. The inclusion of quadratic terms was not supported by the Akaike Information Criterion corrected for small sample sizes (AICc; Table S6). The resulting models fitted the data (likelihood-ratio test: $p < 0.01$). Collinearity was low in the mixed-effects beta regression (variance inflation factors < 2), while collinearity could not be assessed in the Dirichlet regression.

After building models without interactions, (2) we assessed whether the AICc supported the addition of a pairwise interaction, in two separate models: minimum residence time x introduction pathway, minimum residence time x growth form. We then (3) interpreted the supported models by plotting predictions, and used estimated marginal means for the model of niche overlap ('emmeans' package; Lenth, 2023). Finally, we (4) approximated the relative importance of variables with dominance analysis, which calculates the proportional contribution of each explanatory variable to the model's total explained variation ('domir' package; Luchman, 2023).

We did all analyses with R-Studio (version 4.2.0; R Core Team, 2022).

5.4. Results

Overview of climatic niche conservatism components

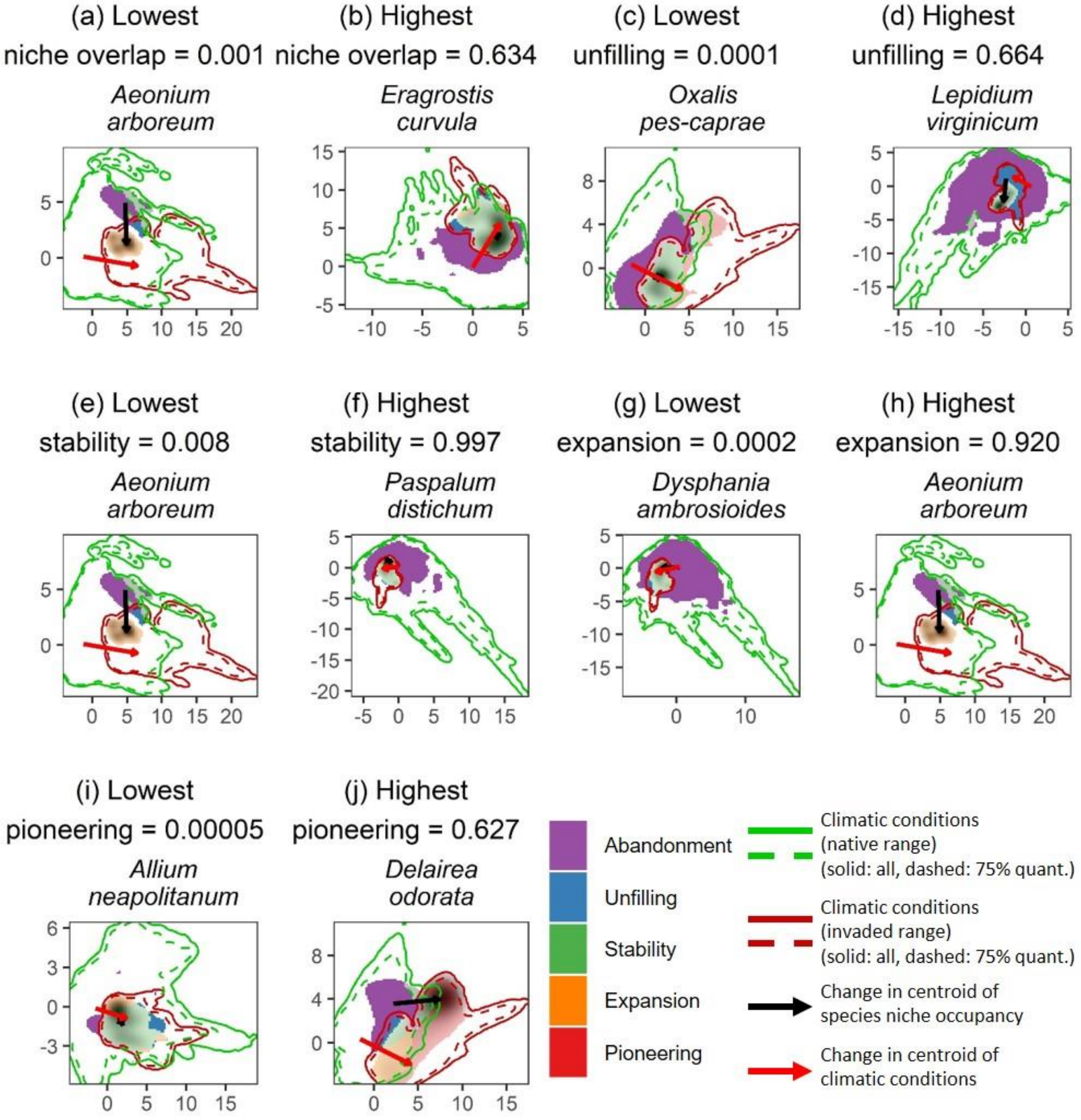

Fig. 5.2. Climatic niches of plant species between the native and invaded ranges, in reduced ordination space (PCA axes), showing only extreme values of metrics of niche conservatism. Except for niche overlap (a) and stability (e), the rest of lowest values excluded zero (c, g, i). Darker shading indicates greater niche occupancy in the invaded range, while grey colour indicates climatic conditions removed from the calculation of niche conservatism metrics, because of their marginality. See Fig. S4.5 for the climatic niches of all species. Abbreviations: quant. = quantile.

Climatic niche conservatism between the native range and the invaded range in Spain was substantial: stability accounted for more than half of niche occupancy in 87% of species (mean = 0.752; Fig. 5.2 and S4.5). Unfilling was generally low (mean = 0.153, 54% of species < 0.1), and twice as large as expansion and pioneering (mean = 0.063 and 0.032, respectively, more than 80% of species < 0.1). Overall, 62% of species showed some evidence of substantially low niche conservatism (unfilling, expansion or pioneering > 0.1). Niche overlap was mostly low (mean Schoener's D = 0.247; Fig. 5.3 and Fig. S4.3).

Correlates of climatic niche conservatism components

Native climatic niche breadth was the most important variable influencing climatic niche conservatism, because it accounted for 61% of the explained variation of niche overlap (mixed-effects beta regression, $R^2_{marginal} = 0.180$), and for 51% of the explained variation of the other climatic niche conservatism components (Dirichlet regression, pseudo-$R^2 = 0.219$). Niche overlap decreased by more than half between the species with the narrowest and the widest climatic niche in their native range (model's predictions; Fig. 5.3). Climatic niche conservatism components changed with increasing native climatic niche breadth: stability increased 19%, expansion and pioneering decreased by 11% and 9% (respectively, model's predictions), unfilling changed around 1% (Fig. 5.4).

Growth form was more important for niche overlap than for the other climatic niche conservatism components: 25% vs 12% of explained variation. Shrubs and trees tended to have 8% less niche overlap than perennial herbs (Tukey contrast on estimated marginal means: p-v = 0.031), and marginally less overlap than annual herbs (p-v = 0.083; Fig. 5.3). Moreover, shrubs and trees tended to have 13% less stability than annual and perennial herbs, and 10% more unfilling (model's predictions; Fig. 5.4), but similar expansion and pioneering (around 1% change). Neither niche overlap nor the other climatic niche conservatism components were explained by the interaction between growth form and minimum residence time (both: ΔAICc > 4, Table S4.8).

Niche overlap was not related to minimum residence time (95% confidence interval included zero, 6% of explained variation, F. 5.3; Table S7). However, minimum residence time influenced the other climatic niche conservatism components (25% of explained variation). Compared to the newest introductions, the oldest introduced species tended to have 20% more stability and 20% less unfilling, while change in expansion and pioneering was around 1% (model's predictions; Fig. 5.4).

Introduction pathway was not important for niche overlap nor the other climatic niche conservatism components (respectively: 8% and 4% of explained variation; both: 95% confidence intervals included zero; Fig. 5.3-5.4). The interaction between introduction pathways and minimum residence time did not explain niche overlap nor the other climatic niche conservatism components (both: ΔAICc > 4, Table S4.8).

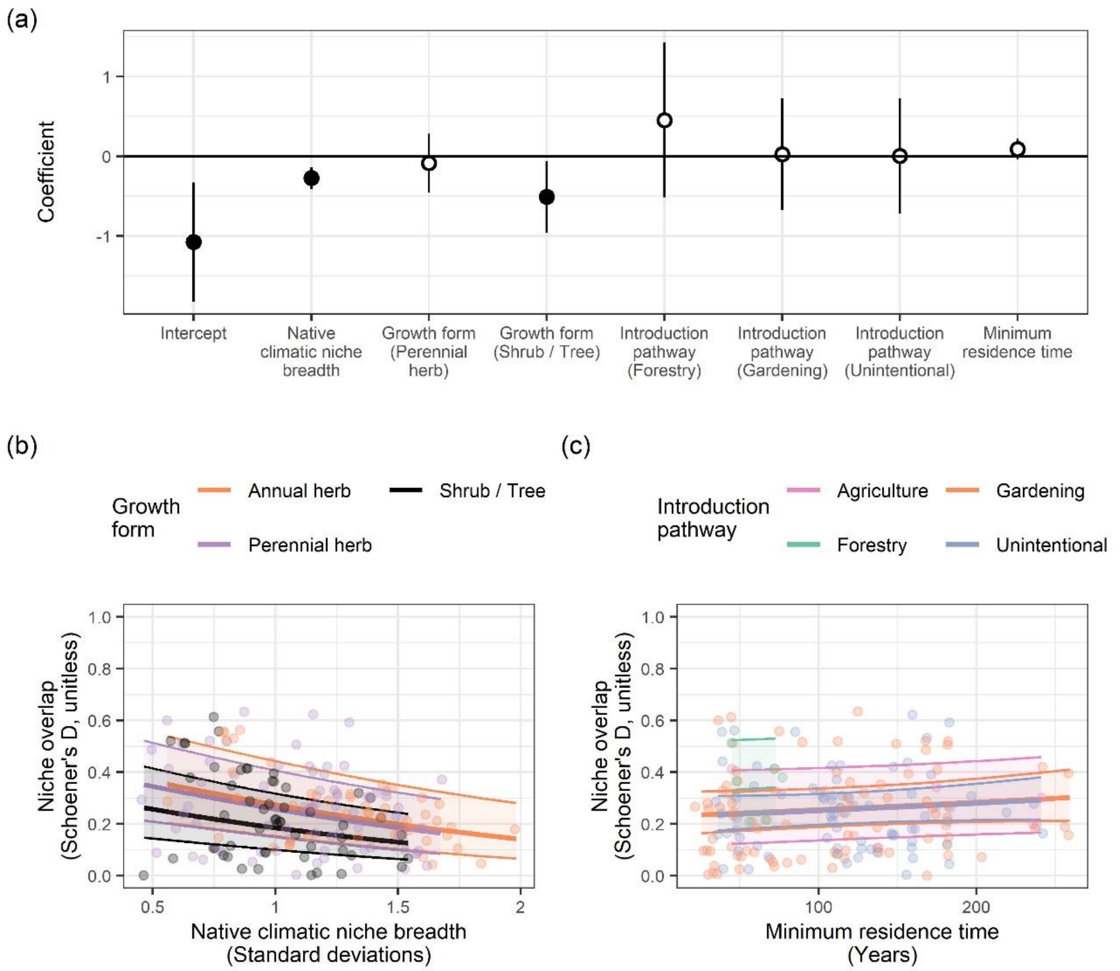

Fig. 5.3. Correlates of niche overlap (Schoener's D), as modelled by a mixed-effects beta regression (genus nested within family), using data up to the 75th quantile. (a) Coefficients at the logit scale, those that included zero in their 95% confidence intervals have white filling. The intercept is the mean niche overlap of plants with the mean value of numerical covariates, and the reference categories of annual growth form, and agricultural introduction pathway. (b-c) Predicted relationships between niche overlap and explanatory variables (with 95% confidence bands, avoiding extrapolation). Dots depict non-native plant species, with added noise and transparency for visualization. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways). See Table S7 for the coefficients.

Phylogenetic relatedness was important for niche overlap, because the random effect of taxonomy (genus nested within family) increased the explained variation four-fold ($R^2_{marginal}$ = 0.180; $R^2_{conditional}$ = 0.654). In comparison, phylogenetic relatedness contributed little to the explained variation on the other niche conservatism components (phylogenetic axis 8: 8%), but still was twice as much as introduction pathways, and close to growth form.

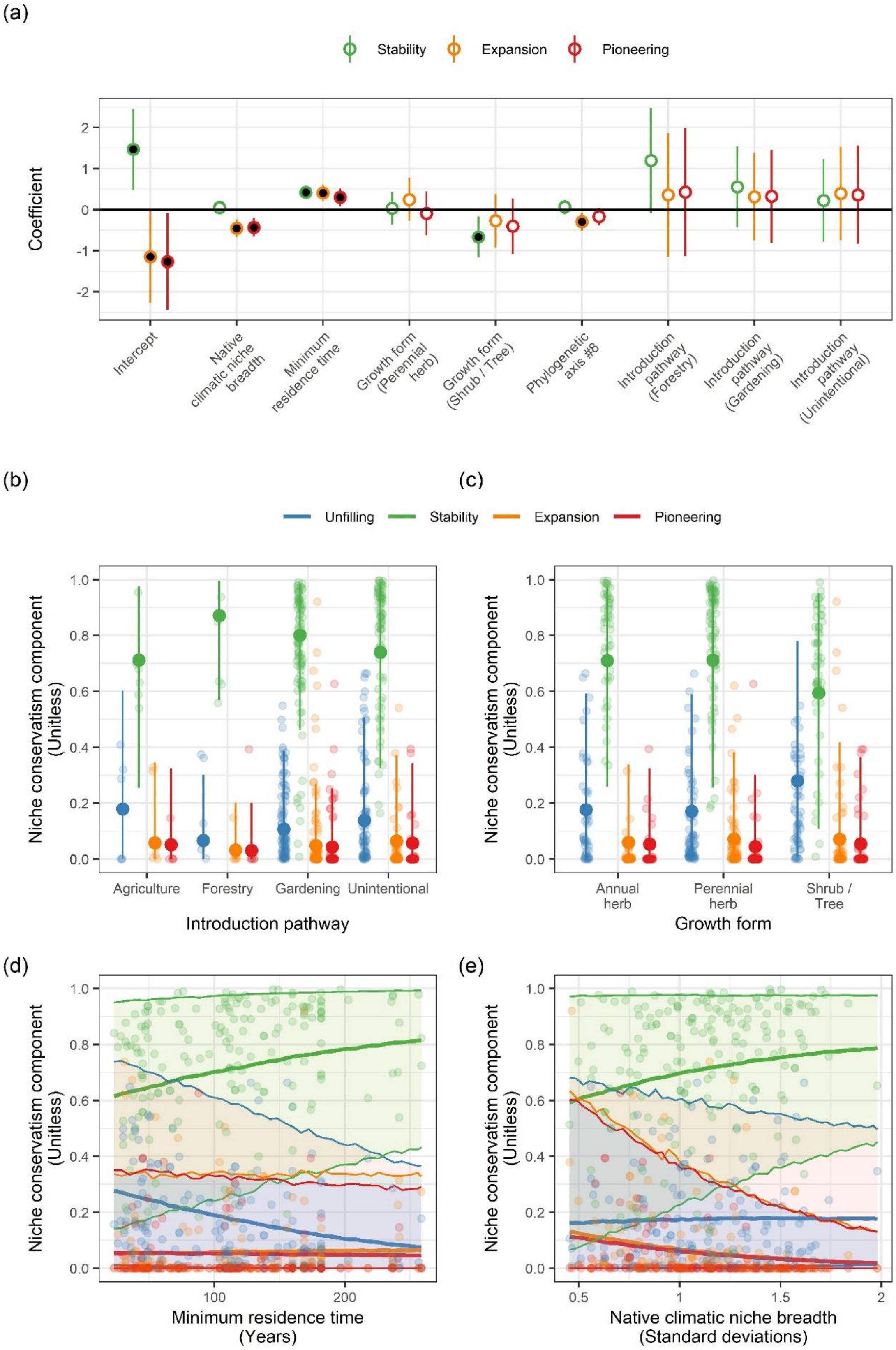

Fig. 5.4. Correlates of the other niche conservatism components, as modelled by a Dirichlet regression, using data up to the 75th quantile. (a) Coefficients at the multinomial logit scale, those that included zero in their 95% confidence intervals have white filling. The intercept is the mean niche conservatism component of plants with the mean value of numerical covariates, and the

reference categories of annual growth form, and agricultural introduction pathway. (b-e) Predicted niche conservatism components, which always sum up to one for each factor level (b-c) and each value of the numerical covariates (d-e). Confidence bands around predicted trends (thick line) are 95% prediction intervals obtained through simulation (Douma & Weedon, 2019). To aid visualization, dots depict non-native plant species with added transparency and random noise (four dots per species), and in panels (b-c), niche conservatism components are plotted side-by-side for each factor level. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways). See Table S4.5 for the coefficients.

5.5. Discussion

Climatic niche differences between the native range and the invaded range in mainland Spain were characterised by high levels of niche stability, while niche overlap was mostly low. Introduction pathways were not correlated to any of the climatic niche conservatism components. Climatic niche conservatism was highest for annual and perennial herbs, plants introduced a long time ago, and those with wide climatic niches in their native range. Climatic niche conservatism was not driven by relevant interactions of introduction pathways nor growth form with minimum residence time. The most important factor influencing climatic niche conservatism was native climatic niche breadth, suggesting that conservatism was more influenced by a species’ ability to cope with broad climatic conditions rather than processes related to introduction history or growth form.

Overview of climatic niche conervatism

Stability was the dominant niche conservatism component, largely supporting the niche conservatism hypothesis, which posits that species tend to retain their niche in time and space (Liu et al., 2020; Petitpierre et al., 2012). Furthermore, our finding of conserved climatic niches are consistent with the invasion of similar habitats between ranges (Kalusová et al., 2013). Niche overlap between the native and the invaded ranges was mostly low, congruent with previous work on non-native plants (Dellinger et al., 2016; Donaldson et al., 2014; Sychrová et al., 2022). Around 40% of plants had relevant levels of niche unfilling, indicating a potential to occupy more climatic space in the invaded range (Liu et al., 2020). Moreover, plants rarely expanded their niche into climatic conditions that were available but not occupied in their native range, and the pioneering into climatic conditions that were not available in their native range was even rarer. This was possibly due to fitness trade-offs among traits, lack of sufficient genetic diversity or dispersal limitations, which prevented occupancy of more extreme climatic conditions (Alexander & Edwards, 2010).

Introduction pathways as correlates of climatic niche conservatism

Contrary to our expectation, and partly in contrast with previous studies (Atwater et al., 2018; Liu et al., 2020), all of the studied niche conservatism components were unrelated to introduction pathways. An analysis considering non-analog climates at the global scale found that wide cultivation correlated to reduced niche overlap, stability and unfilling, and increased expansion (compared to plants that were not cultivated; Atwater et al., 2018). In contrast, in a meta-analysis considering only analog climates, a combination of intentional and unintentional introduction lead to greater niche similarity and stability, but similar expansion and unfilling (compared to plants introduced only intentionally or only unintentionally; Liu et al., 2020). Our work therefore suggests that the effect of introduction pathways on niche conservatism could be context-dependent.

Our results do not support the greater niche overlap for forestry introduced species compared to those introduced for gardening, as reported among *Acacia* species invading South-Africa (Donaldson et al., 2014). Moreover, we did not find relevant interactions between pathways and residence time effecting niche conservatism. The similar niche conservatism among plants introduced through different pathways could relate to multiple explanations. First, introduction pathways are proxies of initial conditions of introduction that can become less relevant to explain invasion patterns as residence time increases (Donaldson et al., 2014; Kempel et al., 2013). Second, we possibly lacked statistical power to detect small effects. Third, agricultural introductions concentrated in earlier years (Riera et al., 2024; Sanz-Elorza, Mateo, et al., 2009), while forestry introductions were very recent, which could hinder the test for an interaction between introduction pathways and minimum residence time. Fourth, introduction pathways were stronger proxies of growth form than native climatic niche breadth (Riera et al., 2024), while the latter was more strongly related to niche conservatism than growth form.

Other correlates of climatic niche conservatism

Growth form was a relevant correlate of climatic niche conservatism, with effects contrary to our expectations: annual and perennial herbs showed more niche stability and overlap than shrubs and trees. Our result agrees with previous findings (Atwater et al., 2018), while other studies found no relationship between niche conservatism and longevity or growth form (Gallagher et al., 2010). The lower niche conservatism for shrubs and trees could relate to covariation with introduction pathways: shrubs and trees were disproportionately likely to be cultivated (Atwater et al., 2018; Riera et al., 2024), which previous work has linked to less stability and overlap (Atwater et al., 2018). Therefore, while we could not recover an individual or interacting effect of pathways on niche conservatism, we cannot rule out an indirect effect through a covariation with growth form (Atwater et al., 2018).

In any case, our results do not support reduced niche conservatism among herbs due to more “evolutionary potential” (i.e. faster rates of molecular and niche evolution; Lanfear et al., 2013; Smith & Beaulieu, 2009). The interaction between growth form and minimum residence time was not an important correlate of niche conservatism, contrary to our expectations, but similarly to previous work (Early & Sax, 2014). The lack of correlation could be due to differences of scale: faster rates of molecular and climatic niche evolution above the genus level across millions of years (Lanfear et al., 2013; Smith & Beaulieu, 2009), do not necessarily translate into reduced niche conservatism at the species level across two and a half centuries of invasion. Moreover, other works approximating “evolutionary potential” found similar niche conservatism between apomictic and sexually reproducing plants (Dellinger et al., 2016). A more proximal test of the role of “evolutionary potential” on niche conservatism would require data on genetic diversity, and the incidence and magnitude of post-introduction evolution (Dellinger et al., 2016).

The importance of minimum residence time on climatic niche conservatism indicates the need of considering the dynamic nature of invasions. As we expected, there was more niche conservatism among older introductions, partly in contrast to previous works (Early & Sax, 2014; Gallagher et al., 2010; Liu et al., 2020; Petitpierre et al., 2012; Sychrová et al., 2022). Niche overlap was unrelated to minimum residence time, similarly to previous works on analog climates (Liu et al., 2020; Petitpierre et al., 2012; Sychrová et al., 2022). Our results provide new insights on patterns of geographical spread and niche breadth. Plants with more residence time tend to achieve greater range size and niche breadth in the invaded range (Banerjee et al., 2021; Gassó et al., 2009; Riera et al., 2024). Since we observed increasing stability and decreasing unfilling with increasing residence time, our results suggest that spread in geographic and climatic space in the invaded range mostly takes place by invading climatic conditions similar to the ones in the native range.

The overwhelming correlate of niche conservatism was the breadth of the climatic niche in the native range: plants with wider native climatic niches had more niche conservatism, as we expected (Dellinger et al., 2016; Early & Sax, 2014; Sychrová et al., 2022; but see Gallagher et al., 2010). Plants with a narrow niche in the native range had more climatic space left to occupy, and their capacity to achieve greater expansion and pioneering could relate to pre-adaptation (Carlin et al., 2023; Petitpierre et al., 2012), post-introduction evolution of adaptation (Early & Sax, 2014), or to an enhancement of their dispersal by human activity (Carlin et al., 2023). The major importance of native climatic niche breadth suggests that plant physiological tolerances arising through natural selection in the native range were more important than features of the introduction process in the invaded range.

Additional factors outside our scope could influence our results. We showed that accounting for phylogenetic relatedness increased explained variation in niche conservatism, a pattern that has not been analysed before (Atwater et al., 2018; Dellinger et al., 2016). Therefore, niche conservatism could be influenced by phylogenetically correlated variables which we did not include in our models, such as functional traits (Vásquez-Valderrama et al., 2022). Niche conservatism can also be influenced by biotic interactions; for instance, the release from herbivores and fungi could allow colonizing environmental conditions that were unoccupied in the native range (DeWalt et al., 2004). Furthermore, the inclusion of non-climatic variables, such as anthropogenic disturbance, could yield further insights (González-Moreno et al., 2015).

Conclusions and implications for management

Our work illuminates how niche conservatism is associated with introduction-related factors and species’ biological attributes. The most important correlate of niche conservatism was native climatic niche breadth, rather than introduction pathways, growth form or minimum residence time. Furthermore, we identified which variables influenced changes in stability and unfilling, which are two niche conservatism components with positive and negative effects on the ability of Ecological Niche Models to predict non-native plant’ spread (Liu et al., 2022). Ecological Niche Models would be most reliable for herbs, species introduced a long time ago, and with wide climatic niches in their native range. Further research is needed into the correlates of niche conservatism among non-native plants, given the accelerating pace of new invasions (Seebens et al., 2018), and ever increasing negative impacts (Bacher et al., 2024).

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Chapter 6

General discussion

This chapter summarizes the discussions addressed in each particular chapter, following the research questions outlined in the Objectives (Section 1.2) as a framework:

Q1. Do introduction pathways determine similar invasion success (i.e. range size) on contrasting species groups?

As addressed in Chapter 2, introduction pathways are one of the few variables that can provide unifying insights on the fate of introduced species across all taxonomic groups (Hayes & Barry, 2008; Pyšek et al., 2020). However, their relationship to invasion success in terms of range size remains poorly explored. This thesis brings the novel result that range size was substantially similar across taxa introduced through different pathways (using five pathway categories). The few significant differences in range size among pathways arose from interactions with minimum residence time, which showed that species introduced a long time ago tended to be more geographically widespread. These results suggest that across taxonomic groups, introduction pathways are weaker proxies of the drivers of geographical spread than time since introduction.

Among taxonomic groups, we observed greater range size over time among species introduced unintentionally as contaminants of commodities than those escaping from cultivation or captivity. Such higher ability to overcome filters to survival, reproduction and dispersal could arise from trait selection. The contaminant pathway would preferentially transport plant and invertebrate species with small seeds or small body size (Gippet et al., 2019; Saul et al., 2017; von der Lippe & Kowarik, 2012). The small size would help species to disperse unnoticed (Gippet et al., 2019), while a previous study found that the small and lightweight seeds of unintentionally introduced plants readily attached to vehicles (von der Lippe & Kowarik, 2012). Therefore, our novel results agree with the idea that unintentional pathways tend to introduce pre-adapted species that associate efficiently with human transport (Pyšek et al., 2011; von der Lippe & Kowarik, 2012).

Species that spread unaided did not become more geographically widespread with increasing residence time, likely reflecting a disadvantage arising from almost no propagule pressure in our study area (by definition), and from the incomplete knowledge of the distribution of terrestrial invertebrates, which often spread unaided (Roques, 2010). Therefore, the pathway-specific differences in range size across animals and plants are consistent with pathway-specific nuances in the features of the introduction process, and in the preferential transport of taxonomic groups and species with certain pre-adaptations.

Q2. Do biological attributes and history modulate pathway effects on plant species success in space and time?

The thesis assessed how plant species biological attributes and minimum residence time modulate the effect of introduction pathways on invasions success. It provides new evidence of associations between biological attributes and pathways, such as a higher incidence of epizoochorous dispersal among unintentionally introduced plants (Chapter 4), which complements previous findings of smaller and more lightweight seeds (von der Lippe & Kowarik, 2012). We also confirm a higher incidence of annual herbs and shorter height among unintentionally introduced plants (Chapters 3, 4 and 5; Lehan et al., 2013;

Pyšek et al., 2011), which is consistent with a higher prevalence of the ruderal adaptive strategy, and lower prevalence of the competitor and stress-tolerating strategies (K. Guo et al., 2022; Lambdon et al., 2008a). This covariation between introduction pathway and growth form could explain the novel finding that unintentionally introduced plants often have wider climatic niches in their native range (Chapters 3, 4 and 5), because herbs often have wider native climatic niches than other growth forms (Banerjee et al., 2021; Smith & Beaulieu, 2009). Therefore, plants introduced through a given pathway often share biological attributes (i.e. a suite of pre-adaptations), giving rise to "functional syndromes" that could modulate the role of pathways on the fate of introduced plants (K. Guo et al., 2022; Pyšek et al., 2011).

The functional syndromes could explain why unintentionally introduced plants achieved similar range size to gardening or agriculture/forestry plants (Chapter 3), or why contaminants of commodities achieved greater range size than plants escaping from cultivation (Chapter 2). The finding of similar range size across pathways is consistent with previous work (Gassó et al., 2009; Harris et al., 2007; Küster et al., 2008; Speek et al., 2011), and suggests that the functional syndrome of unintentionally introduced plants can compensate the lack of cultivation in some circumstances. For instance, unintentionally introduced often have small and lightweight seeds, short height and epizoochorous dispersal, which boost dispersal on vehicles and people's clothing (Ansong & Pickering, 2014; von der Lippe & Kowarik, 2012; Yang et al., 2021). Furthermore, unintentionally introduced plants could become geographically widespread through a higher environmental tolerance, as suggested by their wider climatic niches in their native range (Sheth et al., 2020; Slatyer et al., 2013; Vázquez, 2006). Besides, the higher incidence of an annual life cycle among unintentionally introduced plants would allow them to benefit from windows of opportunity created by anthropogenic disturbance (Davis et al., 2000; Jauni et al., 2015).

A shared introduction history could also explain the similar or larger range size among unintentionally introduced plants compared to intentional introductions (Chapters 3 and 2), through a higher diversity of introduction epicentres. Initial foci of intentional introduction would mostly occur in urban areas, which concentrate gardening activities (Ni & Hulme, 2021; Padayachee et al., 2017). In contrast, initial foci of unintentional introduction would encompass urban areas (final destination of people and commodities), croplands (contaminated seed lots), and transport infrastructures (hitchhikers on people, luggage and commodities; González-Moreno et al., 2013; Harrower et al., 2018). This idea is supported by the contribution of pathways to a regional non-native flora over long time periods (Chapter 3): agricultural introductions decreased in importance and gardening ones increased, while unintentional ones fluctuated. The different temporal trends between agricultural and unintentional introductions suggest that the latter have diversified their introduction epicentres over time, through an increasing association with the global exchange of commodities and people (Cerrato et al., 2023; Sanz-Elorza, Mateo, et al., 2009).

When multiple plant characteristics were modelled, only minimum residence time was significantly correlated to invasion success in terms of range size (Chapter 3). Residence time integrates many factors, since older introductions might have accumulated more generations, or have had their propagules spread by humans for a longer time, leading to greater accumulative propagule pressure (Akasaka et al., 2012; Casado et al., 2018;

Gassó et al., 2009). While residence time could indicate higher chance of evolution in the invaded range (Colautti & Barrett, 2013), a review found that magnitude of local adaptation was unrelated to residence time (Oduor et al., 2016). Overall, the results of the thesis suggest that human-mediated factors like residence time can explain invasion success in terms of range size better than biological attributes and introduction pathways.

Q3. Do pathways affect invaded niche conditions in terms of breadth and harshness?

Non-native plants introduced intentionally or unintentionally achieved similar niche breadth in the invaded range, in terms of habitat range (count of habitat types, Chapters 3 and 4), climatic niche breadth (dispersal of temperature and rainfall in ordination space, Chapters 3 and 4), and biotic niche breadth (degree of habitat specialization through beta-diversity among plots, Chapter 4). Such results could arise through similar mechanisms as those discussed in the previous section, in particular shared biological attributes or functional syndromes, and features of the introduction process.

We also tested the effect of multiple introduction pathways, finding that plants introduced both intentionally and unintentionally achieved greater habitat range in their invaded range than those introduced only unintentionally (but similar climatic and biotic niche breadth, Chapter 4). This thesis provides novel evidence of the functional syndrome of plants with a combined intentional and unintentional introduction: they often had wider climatic niches in their native range, and were introduced earlier (Chapter 4). Moreover, a combined introduction would lead to a higher diversity of introduction epicentres and propagule pressure due to a diversification of the propagule sources (Pergl et al., 2017). These factors could grant an advantage in terms of habitat range through similar mechanisms as those discussed for range size (see previous section).

The importance of introduction pathways at influencing niche breadth was secondary to biological attributes and minimum residence time, regardless of how pathways and niche breadth were measured (Chapters 3 and 4). Minimum residence time increased habitat range (Chapters 3 and 4), climatic niche breadth (Chapter 3, not significant in Chapter 4) and biotic niche breadth (Chapter 4). This largely agrees with previous studies (Banerjee et al., 2021; Fristoe et al., 2021; Lazzaro et al., 2020), although the effect could depend on invasion status (Pyšek et al., 2011). In contrast, native climatic niche breadth was only significantly related to niche breadth in the invaded range in terms of climatic niche (positive effect in Chapter 4, not significant in Chapter 3). This suggests the importance of pre-adaptation to a wide niche, and that niche comparisons between invaded and native ranges might be more informative between similar approximations.

The results of this thesis on niche harshness complement those on niche breadth, by showing how specific niche factors in the recipient location filter the distribution of non-native plants according to their introduction pathway. Overall, the association of pathways with overcoming harsh environmental filters depended on the type of stress, possibly in relation to the functional syndromes outlined in the previous section. Intentional pathways were associated with the invasion of dry habitats, possibly due to higher incidence of plants with a stress-tolerating adaptive strategy (K. Guo et al., 2022;

Lambdon et al., 2008a), such as succulents used in xeriscaping (Bradley et al., 2012; Lambdon et al., 2008a; Sanz-Elorza et al., 2004a). In contrast, pathways were not associated with the invasion of oligotrophic conditions. Moreover, unintentionally introduced plants were associated with the invasion of saline habitats, possibly owing to substantial dispersal ability (epizoochory and lightweight seeds, Chapter 4; von der Lippe & Kowarik, 2012), and an advantage from anthropogenic disturbance (Chapters 3 and 4), which can ameliorate stressful conditions (Lakoba et al., 2021; Zefferman et al., 2015).

However, the results on niche harshness in terms of elevation in the recipient location showed both a positive association with intentional pathways (Chapter 3; Chytrý et al., 2021; Thuiller et al., 2006), and a negative association (Chapter 4; Akatova & Akatov, 2019; McDougall et al., 2011). The disparity of results could arise from methodological differences, as well as from the heterogeneity across mountainous regions (Alexander et al., 2011; McDougall et al., 2011), and regional variation in the proportion of intentionally introduced plants worldwide (van Kleunen et al., 2020). This thesis relied on mixed-models to account for heterogeneity in the correlates of niche harshness among European countries (random intercepts, Chapter 4), but such random effects contributed little to explained variation. This could indicate a complex pattern of heterogeneity at the continental scale that could not be captures by the random intercepts, or that heterogeneity is more relevant at sub-national scales.

Pathway-specific differences in habitat type and land-cover were stronger than those in niche harshness, and showed that anthropogenic habitats (Chapters 3 and 4) and cropland land-cover (Chapter 4, not significant in Chapter 3) were associated with reduced invasion by intentional pathways. These results suggest that anthropogenic disturbance tends to filter unintentionally introduced plants, in line previous research (González-Moreno et al., 2013; Lehan et al., 2013; Ni & Hulme, 2021), and with already-discussed ideas such as functional syndromes (pre-adaptation to anthropogenic disturbance of annuals and ruderals; K. Guo et al., 2022) and different introduction epicenters across pathways (croplands and urban areas; Ni & Hulme, 2021).

Overall, the results on pathway-specific niche differences in non-native plants mimic those with multiple taxonomic groups, in the identification of environmental conditions that facilitate invasion by species introduced through a given pathway (Chapter 2). Therefore, non-native plants appear to concentrate in “invasion hotspots” in geographical and environmental space according to their introduction pathway, in such a way that these areas of concentration of invaders do not exactly overlap (Chapters 2, 3 and 4). Our analysis across taxonomic groups also revealed a high importance of anthropogenic disturbance for increasing the number of taxa introduced through each pathway, although waterbodies were more relevant for the deliberate release of many fish, while species that spread unaided were more present near dispersal corridors (Chapter 2). Furthermore, elevation reduced the number of non-native taxa, but not in a simple way related to pathway intentionality. The negative effect of elevation on the number of non-native taxa was strongest for those deliberately released, and least strong for species that spread unaided followed by escapes from captivity or cultivation, with contaminants of commodities and stowaways on vessels being affected with intermediate effect sizes.

Q4. Do pathways modulate niche conservatism between native and recipient areas?

The results of the thesis also support the niche conservatism hypothesis (Liu et al., 2020), since the average invader tended to occupy similar climatic conditions in the native and invaded ranges (Chapter 5), consistently with the invasion of similar habitats between ranges (Kalusová et al., 2013). This was possibly related to a general lack of sufficient genetic diversity, fitness trade-offs among traits, or dispersal limitations, that prevented invasion of more extreme climatic conditions (Alexander & Edwards, 2010). Moreover, by modelling niche occupancy in non-analog conditions exclusive to the invaded range, the thesis provided a more integrative view of niche occupancy across ranges (Atwater et al., 2018).

Introduction pathways were not significant predictors of niche conservatism (Chapter 5), contrary to previous works that found that cultivation reduced niche conservatism in non-analogue climatic space (Atwater et al., 2018), and to a meta-analyses that found that a combined intentional and unintentional introduction fostered niche conservatism (Liu et al., 2020). Moreover, the results of this thesis do not support greater niche conservatism for forestry plants compared to gardening ones, as reported in *Acacia* species invading South-Africa (Donaldson et al., 2014). Therefore, the effect of pathways on niche conservatism could be context dependent. The lack of effect of pathways could arise from attribute selection, since introduction pathways were stronger proxies of growth form than native climatic niche breadth (Chapters 3, 4 and 5), while the latter was the most important correlate of niche conservatism (Chapter 5).

Similarly to our results on range size and niche breadth, species biological attributes and minimum residence time were more relevant predictors than pathways (Chapter 5). The most important predictor was native climatic niche breadth, which was positively related to niche conservatism, possibly due to less climatic space left to occupy (Dellinger et al., 2016; Early & Sax, 2014; Sychrová et al., 2022). Moreover, older introductions had more conserved niches (Early & Sax, 2014; but see Liu et al., 2020; Petitpierre et al., 2012; Sychrová et al., 2022), through the invasion of climatic space that was already occupied in the native range. In light of positive associations of native climatic niche breadth and minimum residence time with range size and invaded climatic niche breadth (Chapters 2, 3 and 4), we suggest that spread in geographical and climatic space mostly occurs in climatic conditions that are similar to those already occupied in the native range. Herbaceous species had more conserved niches than shrubs and trees (Chapter 5), possibly due to a higher incidence of cultivation (Atwater et al., 2018). Our findings also suggest that although herbs have faster rates of molecular and climatic niche evolution (over millions of years; (

Lanfear et al., 2013; Smith & Beaulieu, 2009), this higher “evolutionary potential” does not lead to a less conserved niche at the scale of centuries.

An integrated view of the role of introduction pathways

The thesis provides evidence of some significant effects of pathways on invasion success in terms of range size and niche breadth. However such effects were often inconsistent and of secondary importance compared to minimum residence time and biological attributes (Fig. 6.1; Chapters 2, 3 and 4). In contrast, pathways were not significantly related to niche conservatism (Chapter 5), but they influenced niche harshness (Chapters 3 and 4). The lack of strong and consistent effects possibly relates to the observation that pathways, among other variables, are proxies of the initial conditions of introduction that could become less important to explain invasion patterns as residence time increases (Donaldson et al., 2014; Kempel et al., 2013).

Previous works found greater range size among intentionally introduced plants (Akasaka et al., 2012; Egawa et al., 2019; K. Guo et al., 2024; W. Guo et al., 2019; Pyšek et al., 2015; van Kleunen et al., 2020). Other studies found that pathway-specific differences in range size and habitat depended on the invasion status (casual-naturalized-invasive; K. Guo et al., 2022; Pyšek et al., 2011), while pathway-specific differences in niche breadth depended on which niche conditions were tested (Thuiller et al., 2012). Therefore, the results of this thesis support two ideas: economic use is not a prerequisite for becoming a successful invader, and that the observed link between introduction pathways and invasion success partly depends on theoretical and methodological choices.

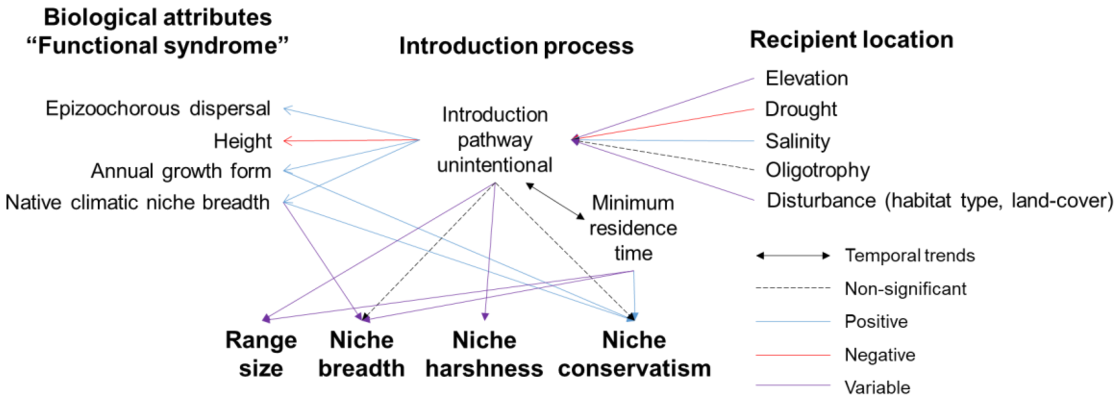


Fig. 6.1. An integrated view on the associations uncovered in this dissertation. For simplicity, the non-significant effects of biological attributes on invasion success are not shown, neither does it show the biological attribute of vegetative reproduction, which was not significantly correlated to introduction pathway.

Range size, habitat range and climatic niche breadth in the invaded range, and niche conservatism were generally not affected by relevant interactions between introduction pathways and selected characteristics (Chapters 3 and 5), while we found some evidence of range size being affected by an interaction between introduction pathway and minimum residence time (Chapter 2, not significant in Chapter 3). These results suggest that the relationship between introduction pathways and the fate of introduced species could be modulated by indirect effects of other drivers of invasion, although synergies could arise in specific circumstances (Chapters 2, 3, and 5).

After being introduced by introduction pathways, non-native species tend to spread over time in geographical and environmental space, in a way that may be significantly influenced by the introduction pathway (Fig. 6.1; Chapters 2, 3 and 4). This process of spread over time culminates in the accumulation of non-native plants in “invasion hotspots” in geographical and environmental space according to their introduction pathway (Chapters 2, 3 and 4). Furthermore, most non-native plants invade climatic conditions that are similar to those already occupied in their native range, to an extent that was not significantly determined by pathways (Chapter 5).

Limitations, future directions and implications for management

This thesis shows that the fate of introduced species depends on the interplay of many causal factors over centuries, and therefore the use of proxies like introduction pathways and minimum residence time is subjected to limitations as conditions for introduction and invasion success change over time. We addressed the uncertainty inherent to the reconstruction of past events through extensive literature review and expert consultation, but we cannot rule out inaccuracies of the pathway classification or of earlier introduction dates. Moreover, the study of macroecological patterns relies on large biodiversity databases that suffer from biases (C. Meyer et al., 2016; Yesson et al., 2007), which we sought to reduce following guidelines (Knollová et al., 2005; Zizka et al., 2019).

The explanatory power could increase by modelling additional key variables, which could be phylogenetically correlated, as suggested by an important phylogenetic signal in some of the analyses of this thesis (Ives, 2022). A key variable could be propagule pressure, but historical data is largely restricted to cultivated plants (Richardson & Pyšek, 2012). Future work could explicitly model direct and indirect effects of variables, thus assessing how a variable mediates the effect of another (K. Guo et al., 2024). Moreover, a causally explicit framework grounded in ecological theory that considers confounders could identify the causes of context dependence (Catford et al., 2022).

This thesis also provides insights to better manage non-native invasive species, following the rule of thumb that management efforts should be prioritized according to the stage of invasion (prevention vs. eradication/containment; McGeoch et al., 2016). The finding of substantial similarities in invasion success across pathways (Chapters 2, 3 and 4), supports a preventive strategy that encompasses both types of introduction. Moreover, new introductions could be prevented in invasion hotspots by implementing measures tailored to each pathway (Chapters 2, 3 and 4). For instance, by preventing the sale of priority invaders in urban areas, or enforcing biosecurity measures in trade infrastructures. If prevention fails, the results on minimum residence time support early detection schemes and a rapid eradication of priority species, possibly focusing on hotspots of invasion (Chapters 2, 3 and 4). The priority species for prevention and eradication often possess attributes related to high invasion success, such as wide climatic niches in their native range, or a combined intentional and unintentional introduction (Chapter 4). If eradication does not occur, containment efforts could be optimized to suitable areas identified by Ecological Niche Models, which would be most reliable for plants with wide native climatic niches, herbaceous growth form and old introduction (Chapter 5). The management of well-established invaders could be prioritized in sites of high conservation value that overlap with hotspots of invasion.

Lastly, the change over time in pathway importance suggests the need for flexible management strategies that keep ahead of socio-economic changes (Chapter 3).

General conclusions

This section summarizes the main conclusions of the thesis, mostly developed in different chapters but sometimes shared and further developed in the previous section:

Plants and animals introduced through different pathways tended to achieve similar invasion success in terms of range size, with two exceptions arising from interactions with minimum residence time. Those introduced unintentionally as contaminants of commodities became more geographically widespread over time than those escaping from captivity or cultivation, while those spread unaided did not become more geographically widespread over time (Chapter 2).

Pathway-specific differences in invasion success across animals and plants, in terms of range size, are consistent with pathway-specific nuances in the features of the introduction process, and in the preferential transport of taxonomic groups and species with certain pre-adaptations. Contaminants of commodities could be pre-adapted to anthropogenic dispersal due to small size and low detectability, while those spreading unaided would not benefit from propagule pressure and could be underrecorded (Chapter 2).

Non-native plants introduced unintentionally achieved similar or even higher invasion success, in terms of range size, than those plants introduced intentionally. Similarly, invasion success in terms of niche breadth was largely unrelated to introduction pathway, independently of whether niche breadth in the invaded range was assessed through habitat range, climatic niche breadth, or biotic niche breadth. However, plants introduced both intentionally and unintentionally invaded a higher number of habitats than those introduced only unintentionally. Overall, economic use does not appear as a necessary prerequisite of invasion success (Chapters 2, 3 and 4).

Pathway-specific differences in invasion success across plants were modulated by shared species biological attributes (functional syndromes), and features of the introduction process. Compared to intentionally introduced plants, unintentionally introduced plants tended to be shorter and to have wider climatic niches in their native range, and were also more likely to be epizoochorous and annual herbs. Moreover, plants introduced both intentionally and unintentionally were likely to be herbs, and tended to be short with wide native climatic niches and longer residence time (Chapters 3, 4 and 5).

Introduction pathways underwent substantial changes over time, mimicking socio-economic changes, with potential implications on the fate of introduced plants. Temporal trends in pathway importance indicate a decoupling between agricultural and unintentional introductions, while gardening ones rose considerably. The intensification of the global exchange of commodities and people probably lead to diversification of introduction epicentres of unintentional introductions over time, encompassing both croplands and urban areas (Chapter 3).

Introduction pathways were of secondary importance to explain invasion success when species attributes or features of the introduction process were also modelled. Minimum residence time was a relevant predictor of range size across animals and plants, and was also associated with niche breadth among plants, with a consistent effect: older introductions tended to be more successful. A relevant species attribute was the breadth of the climatic niche in the native range, which was positively associated with climatic niche breadth in the invaded range (Chapters 2, 3 and 4).

Animals and plants introduced through different pathways tended to invade slightly different types of environmental conditions, as shown by low overlap among hotspots of invasion across pathways. Anthropogenic disturbance generally increased the number of taxa introduced through different pathways, although waterbodies were relevant for deliberate release of many fish, while species that spread unaided were more present near dispersal corridors (Chapter 2).

Pathway-specific niche differences were also observed among non-native plants, showing that filtering exerted by niche harshness depended on the type of stress. Dry conditions were mostly invaded by intentionally introduced plants, while saline conditions were mostly invaded by unintentionally introduced ones. The link between pathway intentionality and the invasion of high elevations was inconsistent across studies, hinting at context dependent and complex relationships (Chapters 3 and 4).

Pathway-specific differences in habitat type and land-cover were more relevant than those in niche harshness. Unintentionally introduced plants were the majority of invaders in anthropogenic habitats, while they also became more prevalent with greater cropland land-cover in some circumstances (Chapters 3 and 4).

Non-native plants largely supported the niche conservatism hypothesis, since they invaded similar climatic conditions in their native and invaded ranges. We did not find an important role of pathways, which were of secondary importance to species biological attributes and minimum residence time (Chapter 5).

The most important correlate of niche conservatism was the breadth of the native climatic niche. Non-native plants with wider niches in their native range tended to have more stable niches. Furthermore, the niche tended to be more conserved among plants with herbaceous growth form and those introduced a long time ago (Chapter 5).

Across non-native plants, the effect of introduction pathways on range size, niche breadth and niche conservatism was largely unaffected by interactions with selected species biological attributes and features of the introduction process. However, range size across animals and plants was significantly affected by an interaction between introduction pathway and minimum residence time. Therefore, the relationship between pathways and the fate of introduced species could be indirectly modulated by other variables, yet synergies could arise in specific circumstances (Chapters 2, 3, and 5).

Appendix 1

Supplementary Material for Chapter 2

This Appendix contains

Tables S1.1-S1.6

Figures S1.1-S1.3

Supplementary Discussion

Supplementary tables

Table S1.1. Neobiota in Catalonia (i.e. alien species introduced after 1500), including for each species: introduction pathways, minimum residence time, range size (number of occupied 10-km UTM cells), and bibliographic sources. Species are pooled in synthetic taxonomic groups: aquatic invertebrates, aquatic vertebrates, plants, terrestrial vertebrates and terrestrial vertebrates. Subgroups are provided for vertebrates as provided by the EXOCAT database (http://exocatdb.creaf.cat/base_dades/). Aquatic status for plants was taken from the Atlas of invasive flora of Spain (Sanz-Elorza et al., 2004a). Species are listed alphabetically within each group or subgroup. Abbreviations: Rel = Release, Esc = Escape, Con = Contaminant, Sto = Stowaway, Un = Unaided, RS = range size (number of occupied 10-km UTM cells), MRT = Minimum Residence Time (calculated as the difference between the year of writing [2019] and the first record in the wild).

(a) Aquatic invertebrates (N = 22 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Ankylocythere sinuosa			1			11	2	Parasite probably introduced with contaminated *Procambarus clarkii* (Aguilar-Alberola et al., 2012). MRT from the literature (Aguilar-Alberola et al., 2012).
Austropeplea viridis			1			4	1	Probably introduced via aquaculture or with plants (Schniebs et al., 2017). MRT from the literature (Schniebs et al., 2017).
Corbicula fluminalis				1		5	5	Pathway uncertain (Quiñonero & López, 2014). Since it probably is an unintentional introduction, we assign the Stowaway pathway, which is common in freshwater invaders. MRT from the literature (Quiñonero & López, 2014).
Corbicula fluminea		1		1		22	61	Introduced with ballast water, and as live food and live bait (Ministerio para la Transición Ecológica, 2013). Aquaculture and the aquarium trade have also been reported (Andreu et al., 2011). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Cordylophora caspia				1		8	1	Introduced with ballast water and hull fouling (Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Craspedacusta sowerbyi			1			42	14	Pathway uncertain, possibly an accidental introduction with plants for the aquarium trade, further spread by translocation of fishes and angling equipment (M. Campos et al., 2013). MRT from the literature (M. Campos et al., 2013).

Dreissena polymorpha				1		18	54	Introduced with ballast water and angling equipment (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Andreu et al., 2011).
Dugesia tigrina			1			49	3	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Baguñà et al., 1980).
Ferrissia (Kincaidilla) fragilis			1			62	13	Commonly found in decaying plant material and the underside of the floating leaves of water lilies (Altaba et al., 1985) sub *Ferrisia wautieri*. Thus, we find reasonable to think it was introduced with plant material or aquatic plants as a Contaminant. MRT from the literature (Altaba et al., 1985).
Galba cubensis			1			4	1	Likely escaped from an horticultural facility (Schniebs et al., 2018). MRT from the literature (Schniebs et al., 2018).
Gyraulus chinensis			1			24	5	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Lernaea cyprinacea			1			24	8	Parasite introduced via aquaculture (Andreu et al., 2011). MRT from the literature (Sánchez-Hernández, 2017).
Melanoides tuberculatus		1				10	4	Introduced through the aquarium trade as an ornamental (Andreu et al., 2011; Ministerio para la Transición Ecológica, 2013). MRT from the literature (Andreu et al., 2011).
Orconectes limosus	1					9	2	Released for fishing (M. Campos et al., 2013; Ministerio para la Transición Ecológica, 2013). MRT from the literature (M. Campos et al., 2013).
Pacifastacus leniusculus	1	1				19	32	Released for fishing and escaped from aquaculture (Ministerio para la Transición Ecológica, 2013), also used as live bait (M. Campos et al., 2013). MRT from the literature (Andreu et al., 2011).
Physella acuta			1			99	22	Introduced in Europe with the cotton trade around 1805, but modern dispersion related to domestic aquaria and the trade of aquatic plants (Quiñonero & López, 2013). MRT from the literature (Quiñonero & López, 2013).
Planorbella duryi		1	1			36	5	Introduced accidentally with imported tropical plants or irresponsibly dumped from domestic aquaria (Quiñonero, López, Ruiz, et al., 2014). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Pomacea insularum		1				10	10	Introduction related to aquaculture or the aquarium trade (Andreu et al., 2011). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Potamopyrgus antipodarum				1		83	173	Introduced with ballast water and angling (Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Procambarus clarkii	1	1				40	245	Released for improvement of wild stocks and escaped from aquaculture (Ministerio para la Transición Ecológica, 2013). MRT from (Ministerio para la Transición Ecológica, 2013).
Pseudosuccinea columella			1			43	2	Introduced mainly in greenhouses (Altaba et al., 1988), where it probably has reached as a Contaminant of imported plant material or soil. MRT from the literature (Altaba et al., 1988).
Sinanodonta woodiana			1			13	8	Accidentally introduced with exotic fishes (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Ministerio para la Transición Ecológica, 2013).

(b) Aquatic vertebrates: amphibians (N = 9 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Bufo mauritanicus		1				36	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from (Andreu et al., 2011).
Cynops pyrrhogaster		1				34	2	This species is part of the international pet trade (Herrel & Van Der Meijden, 2014) and there have been introductions elsewhere in Spain (Pleguezuelos et al., 2002). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Discoglossus pictus					1	62	66	It was first introduced in France (first record in 1906), and subsequently spread into Catalonia (Llorente et al., 2015). MRT from the literature (Llorente et al., 2015).
Ichthyosaura alpestris		1				40	5	The origin of recent populations is unknown, but probably linked to an escape from captivity (Fibla et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Lissotriton boscai		1				11	1	Introduced from NW Iberia (Amat & Carranza, 2011). This amphibian is an Iberian endemic naturally present in the western half of the Iberian Peninsula (Pleguezuelos et al., 2002). We consider the most likely pathway to be an Escape. MRT from the literature (Amat & Carranza, 2011).

Lithobates catesbeianus		1				20	2	Introduced in Spain mainly to be bred in captivity for human consumption, both legally and illegally (Ministerio para la Transición Ecológica, 2013; Pleguezuelos et al., 2002). This species is also kept as a pet (N. Franch et al., 2019; Ministerio para la Transición Ecológica, 2013). In Catalonia it was first reported in 1999 (Andreu et al., 2011), the origin of this first population being uncertain and probably unrelated to breeding farms (Cabana & Fernández, 2010). In 2010 two larvae of this frog were detected in a pet shop in Catalonia, they were linked to the importation of contaminated fish larvae from Italy (Cabana & Fernández, 2010). After 2010 there were only two new records of this species in Catalonia, both in the Ebro delta (N. Franch et al., 2019), over 100 km South of where it was reported as a contaminant in a pet shop. The origin of the Ebro populations has been linked to irresponsible dumping (N. Franch et al., 2019), and we find this pathway likely for the first record of 1999. MRT from the literature (Andreu et al., 2011).
Ommatotriton ophryticus		1				8	2	Recent research has shown that the Catalan population is made up of hybrids between *O. ophryticus* and *O. nesterovi*, that likely interbred in the pet trade (van Riemsdijk et al., 2018). MRT from the literature (Fontelles et al., 2011).
Triturus cristatus		1				2	1	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Xenopus laevis		1				12	1	Introduced for research purposes and as a pet (Ministerio para la Transición Ecológica, 2013; Pascual et al., 2007). MRT from the literature (Pascual et al., 2007).

(c) Aquatic vertebrates: aquatic fish

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Abramis brama	1					15	1	Introduced by anglers (Benejam et al., 2005). MRT from the literature (Benejam et al., 2005).
Acipenser baerii	1	1				24	1	Escape from aquaculture (Elvira & Almodóvar, 2001) and released for recreational fishing (N. Franch, 2012). MRT from the literature (Elvira & Almodóvar, 2001).
Alburnus alburnus	1	1				27	118	Released as a forage species and used as live bait (Elvira & Almodóvar, 2001; Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Ameiurus melas	1	1				109	61	Released for fish stocking, also used as live bait (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). Rarely kept in aquariums (M. Campos et al., 2013). MRT from the literature (Elvira, 1995).
Aphanius fasciatus		1				22	4	Introduced by aquarists (Elvira & Almodóvar, 2001). MRT from the literature (Elvira & Almodóvar, 2001).
Blicca bjoerkna	1					24	11	Released as a forage species (Elvira & Almodóvar, 2001). MRT from the literature (Elvira & Almodóvar, 2001).
Carassius auratus		1				107	120	Introduced as ornamental (Elvira, 1995), also used as live bait (M. Campos et al., 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Carassius carassius	1	1				106	17	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Carassius gibelio		1				107	26	This specie is similar to *Carassius auratus*, and sometimes considered a synonym (Doadrio, 2002). The pathway and MRT assigned to this species are taken from *C. auratus*.
Cobitis bilineata	1	1				24	5	Introduced for recreational fishing (Doadrio et al., 2011), also used as live bait and kept in aquaria (M. Campos et al., 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Ctenopharyngodon idella	1	1				14	3	Introduced through the aquarium trade (López et al., 2012; Maceda-Veiga et al., 2013) and recreational fishing (EXOCAT database, http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Andreu et al., 2011).
Esox lucius	1					65	56	Introduced for recreational fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Fundulus heteroclitus		1				14	5	Introduced by aquarists (Elvira & Almodóvar, 2001; Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Gambusia holbrooki	1					55	122	Introduced for mosquito control (Elvira & Almodóvar, 2001; Ministerio para la Transición Ecológica, 2013). Additional pathways (recreational fishing, aquaculture, aquarists) have been reported (M. Campos et al., 2013), we choose to only assign the Release pathway

								since mosquito control would take precedence over more recent pathways. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Gobio occitaniae		1				6	24	Origin of the introduction uncertain, probably for use as live bait (Aparicio et al., 2013). MRT from the literature (Aparicio et al., 2013).
Hypostomus plecostomus		1				27	2	Ornamental species (Maceda-Veiga et al., 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Ictalurus punctatus		1				24	12	Escape from aquaculture (Elvira & Almodóvar, 2001); also probably introduced as live bait (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Elvira & Almodóvar, 2001).
Lepomis gibbosus	1	1				109	95	Introduced for fish stocking (Elvira, 1995), more recently as live bait and irresponsibly dumped from captivity (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Elvira, 1995).
Leuciscus aspius	1					2	1	Released for fishing (Merciai et al., 2018). MRT from the literature (Merciai et al., 2018).
Leuciscus idus		1				16	2	Introduced through the aquarium trade (López et al., 2012; Maceda-Veiga et al., 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Micropterus salmoides	1					54	139	Released for fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). It has also been reported as live bait (M. Campos et al., 2013), but this pathway appears to be a minor one and we are not including it in the present paper. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Misgurnus anguillicaudatus		1				18	15	The most likely pathways are the aquarium trade and its use as live bait (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Ministerio para la Transición Ecológica, 2013).
Oncorhynchus mykiss	1	1				109	118	Released for fishing (Elvira, 1995) and escaped from aquaculture (Doadrio, 2002). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Perca fluviatilis	1					28	30	Mainly released for fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). Occasionally used as live bait (M. Campos et al., 2013), but this pathway appears to be a minor one and we are not including it in the analysis. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Phoxinus septimaniae		1				37	62	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from databases for *Phoxinus* spp. (Ferrer, 2019).

Pseudorasbora parva		1				20	34	Origin uncertain, probably an Escape from aquaculture (Caiola & Sostoa, 2002; Ministerio para la Transición Ecológica, 2013), additional pathways include the aquarium trade (López et al., 2012) and its use as live bait (M. Campos et al., 2013). MRT from the literature (López et al., 2012).
Pygocentrus nattereri		1				6	1	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Rutilus rutilus	1	1				109	77	Released for fishing (Elvira, 1995) and probably also as a forage species (Ministerio para la Transición Ecológica, 2013). Also used as live bait (M. Campos et al., 2013). MRT from the literature (Elvira, 1995).
Salvelinus fontinalis	1					109	11	Released for fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Salvelinus umbla	1					4	2	Probably released for fishing (Aparicio, 2015). MRT from the literature (Aparicio, 2015).
Sander lucioperca	1					39	37	Mainly released for fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). MRT from the literature (M. Campos et al., 2013).
Scardinius erythrophthalmus	1	1				109	127	Most likely pathway is Release for fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013); also used as live bait and can Escape from aquaculture (M. Campos et al., 2013). MRT from the literature (Elvira, 1995).
Silurus glanis	1					34	48	Released for fishing (Elvira, 1995; Ministerio para la Transición Ecológica, 2013). MRT from the literature (López et al., 2012).
Xiphophorus sp.		1				12	1	Introduced through the aquarium trade (López et al., 2012; Maceda-Veiga et al., 2013). MRT from the literature (López et al., 2012).

(d) Plants: terrestrial plants (N = 520 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Abies pinsapo		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Abutilon grandifolium		1				12	1	Probably an escape from cultivation (Verloove & Gullón, 2008). MRT from the literature (Verloove & Gullón, 2008).

Abutilon theophrasti			1			120	191	Probably introduced as a seed contaminant (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Acacia dealbata		1				35	53	Introduced through cultivation, mainly as ornamental (Casasayas, 1989; Sanz-Elorza et al., 2004a). Less frequently planted for erosion control (Sanz-Elorza et al., 2004a). We assign the Escape pathway since it's use as ornamental appears to be the predominant pathway. MRT from the literature (Casasayas, 1989).
Acacia farnesiana		1				22	16	Escaped from cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Acacia karroo		1				30	3	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Acacia longifolia	1	1				30	5	Introduced as ornamental and for dune stabilisation (Casasayas, 1989; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Acacia melanoxylon		1				30	4	Introduced as ornamental (Casasayas, 1989). Also introduced for dune stabilisation (Sanz-Elorza et al., 2004a), but since this pathway is not mentioned in Casasayas (1989) we assign only the Escape pathway. We give preference to the work of Casasayas (1989) because it focused on the study region of the present paper (it can better reflect the regional idiosyncrasies of the study region of Catalonia). MRT from the literature (Casasayas, 1989).
Acacia retinodes		1				30	8	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Acacia rostellifera		1				6	1	Possibly introduced through cultivation (Álvarez et al., 2016). MRT from the literature (Álvarez et al., 2016).
Acacia saligna		1				30	16	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Acer negundo		1				126	178	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Achillea biebersteinii		1				19	1	Possibly introduced as ornamental or as a seed contaminant (Soriano, 2002), we think an introduction through gardening is more likley. MRT from the literature (Soriano, 2002).
Achillea filipendulina		1				23	6	Introduced as ornamental (Aymerich, 2017). MRT from the literature (Pedrol et al., 2002).

Achillea ligustica		1				40	3	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from databases (X. Font, 2019).
Achillea ptarmica		1				4	1	Escaped from gardens (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Aeonium arboreum		1				35	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Bolòs & Vigo, 1984).
Aesculus hippocastanum		1				106	26	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Agave americana		1				257	198	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Agave fourcroydes		1				6	2	Introduced for agriculture and as an ornamental (Sáez & Guillot, 2014). MRT from the literature (Sáez & Guillot, 2014).
Ageratum houstonianum		1				77	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Ailanthus altissima	1	1				117	323	Introduced as ornamental and for erosion control (Casasayas, 1989; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Albizia julibrissin		1				13	3	Introduced through gardening (Oliver, 2009). MRT from databases (X. Font, 2019).
Alnus alnobetula					1	27	1	Spread from France, where it was introduced through cultivation (Benito et al., 1995). MRT from the literature (Benito et al., 1995).
Alnus cordata		1				111	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Aloe arborescens		1				17	6	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Aloe ferox		1				12	1	Introduced as ornamental (Pyke, 2008). MRT from the literature (Pyke, 2008).
Aloe maculata		1				173	30	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Aloe vera		1				35	1	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Alternanthera caracasana			1			47	22	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Casasayas, 1989).

Alternanthera pungens			1			66	31	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly as a seed contaminant, like it has been suggested in a neighbouring Spanish region (Peña & Ferrer-Gallego, 2016). MRT from the literature (Casasayas, 1989).
Althaea hirsuta subsp. *longiflora*			1			69	1	Unintentional introduction (Bolòs et al., 2005), we think possibly as a contaminant, like it has been suggested in Belgium for *Althaea hirsuta* (Verloove, 2006a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Amaranthus albus			1			142	324	Probably introduced as a seed contaminant (Masalles et al., 1996; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Amaranthus blitoides			1			107	336	Probably introduced as a seed contaminant (Casasayas, 1989; Masalles et al., 1996; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Amaranthus blitum subsp. *emarginatus*			1			34	27	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Casasayas, 1989).
Amaranthus caudatus		1				116	2	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Amaranthus cruentus		1				108	83	Escaped from gardens (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Amaranthus deflexus			1			152	333	Probably introduced as a seed contaminant (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Amaranthus hybridus			1			139	339	Unintentional introduction linked to trade, possibly as a seed contaminant (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Amaranthus hypochondriacus		1				30	67	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Amaranthus muricatus				1		110	212	First introduced unintentionally by trade in a neighbouring Spanish region (maybe as a seed or as packaging material), from where it spread into Catalonia, possibly with the transport of commodities by train or road (Casasayas, 1989; Sanz-Elorza et al., 2004a). Since the spread of this species appears to be linked to transport rather than an ecological association with specific commodities, we assign the Stowaway pathway. MRT from the literature (Casasayas, 1989).
Amaranthus palmeri			1			92	5	Introduced as a contaminant of cotton (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Amaranthus powellii			1			36	149	Introduced as a weed (Casasayas, 1989; Sanz-Elorza et al., 2004a), we think possibly as a seed contaminant. MRT from the literature (Casasayas, 1989).
Amaranthus retroflexus			1			172	374	Two hypotheses have been put forward regarding the introduction of this species: escape from cultivation in botanical gardens or contaminant of agricultural products (Casasayas, 1989; Sanz-Elorza et al., 2004a). We think an introduction as a contaminant is more likely, following Masalles et al. (1996). MRT from the literature (Casasayas, 1989).
Amaranthus spinosus			1			102	17	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly as a contaminant like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Casasayas, 1989).
Amaranthus viridis			1			115	115	Origin of the introduction uncertain, possibly as a seed contaminant (Sanz-Elorza et al., 2004a). MRT from the literature (Sanz-Elorza et al., 2004a).
Ambrosia artemisiifolia			1	1		13	1	The introduction and spread of this species in Europe follows a combination of the Contaminant of seeds, grain and soil; and Stowaway pathways, by agricultural machinery, vehicles, along railroads (Bullock et al., 2012; Buttenschøn et al., 2009). Natural dispersion is relevant (especially along waterways) but less important than anthropogenic processes (Bullock et al., 2012), so it is not included in the present paper. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Ambrosia coronopifolia			1	1		58	75	Unintentional introduction (Sanz-Elorza et al., 2004a). The spread of this species seems to be similar to *Ambrosia artemisiifolia* (Buttenschøn et al., 2009), so we assign the contaminant and stowaway pathways. MRT from the literature (Casasayas, 1989).
Ambrosia tenuifolia				1		69	40	Probably introduced to Europe (in France) with ship ballast, posteriorly spread into Catalonia by railway (Casasayas, 1989). MRT from the literature (Montserrat, 1954).
Amelichloa caudata			1			16	7	Probably introduced as a wool contaminant (Verloove, 2005a). MRT from the literature (Verloove, 2005a).
Amorpha fruticosa		1				21	1	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Gestí & Fàbregas, 2000).
Apium leptophyllum			1			34	5	Possibly introduced as a seed contaminant (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Aptenia cordifolia		1				107	31	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Aptenia lancifolia		1				12	1	Escaped from a botanical garden (Guillot, 2011). MRT from the literature (Guillot, 2011).
Araujia sericifera		1				57	183	Introduced through cultivation (Casasayas, 1989). MRT from databases (X. Font, 2019).
Arctotheca calendula		1				40	22	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Aristolochia sempervirens		1				8	2	Previously recorded in the Iberia Peninsula from Portugal, as an escape from a botanical garden (de Almeida, 1999). Since in Catalonia it has been found near a botanical garden, we assign the escape pathway. MRT from the literature (Pyke, 2013).
Artemisia abrotanum		1				35	6	Introduced through cultivation (Casasayas, 1989). MRT from databases (X. Font, 2019).
Artemisia annua			1			40	36	Unintentional introduction (Casasayas, 1989; Sanz-Elorza et al., 2004a), we think possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2005a). MRT from the literature (Casasayas & Masalles, 1981).
Artemisia arborescens		1				137	40	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Artemisia canariensis		1				30	1	Escaped from gardens (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Artemisia dracunculus		1				38	1	Escaped from gardens (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Artemisia verlotiorum			1			106	312	Introduced to Europe as ornamental. Origin of the introduction to Spain uncertain, maybe through cultivation or unintentional (Sanz-Elorza et al., 2004a). Casasayas (1989) considers this species a weed, and suggests that it mainly spreads by means of its rhizome (which can be mixed with soil and accidentally transported). We assign the contaminant pathway. MRT from the literature (Sanz-Elorza et al., 2004a).
Asparagus asparagoides		1				4	4	Introduced as ornamental (Aymerich, 2015b). MRT from the literature (Aymerich, 2015b).

Asparagus setaceus		1				30	2	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Asparagus sprengeri		1				30	5	Introduced as ornamental (Casasayas, 1989), sub *Asparagus densiflorus*. MRT from the literature (Casasayas, 1989).
Aster novi-belgii		1				90	117	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Aster pilosus		1				67	111	Despite displaying aesthetic and ornamental flowering, Casasayas (1989) never saw it cultivated in Catalonia, and concluded an unintentional introduction was more likely. Nevertheless, in a latter paper (Casasayas, 1990) an introduction as ornamental was suggested. Although considered an unintentional introduction in Spain (Sanz-Elorza et al., 2004a), we give preference to the work of Casasayas (1990) because it could have incorporated new data and it focused on the study region of the present paper (it can better reflect the regional idiosyncrasies of the study region of Catalonia). An introduction through cultivation is reported from Belgium (Verloove, 2005a). MRT from the literature (Casasayas, 1989).
Aster squamatus			1			107	320	Unintentional introduction linked to trade (Sanz-Elorza et al., 2004a), probably as a seed contaminant (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Astragalus boeticus		1				6	1	Possibly introduced through agriculture (Álvarez et al., 2016). MRT from the literature (Álvarez et al., 2016).
Atriplex micrantha			1			52	8	Probably introduced as a wool alien (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Atriplex semibaccata		1				6	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Álvarez et al., 2016).
Atriplex tatarica			1			110	2	We think it was possibly introduced with trade as a contaminant, as it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Aymerich, 2016).
Aubrieta columnae		1				6	1	Possibly introduced as an ornamental (Aymerich, 2016). MRT from the literature (Aymerich, 2014).
Axonopus compressus		1				8	1	Introduced through gardening and agriculture (Giraldo-Cañas, 2008). MRT from the literature (Pyke, 2013).
Baccharis halimifolia		1				14	6	Introduced as ornamental (Barriocanal et al., 2005; Sanz-Elorza et al., 2004a). MRT from the literature (Barriocanal et al., 2005).

Bauhinia grandiflora		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Bergenia crassifolia		1				6	2	Escaped from gardens (Aymerich, 2013c, 2016). MRT from the literature (Aymerich, 2013c).
Berteroa incana			1			32	2	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Aymerich, 2016).
Bidens aurea			1			56	110	Unintentional introduction probably linked to trade (Casasayas, 1989; Sanz-Elorza et al., 2004a), we think possibly as a contaminant of seeds or wool. MRT from the literature (Casasayas, 1989).
Bidens frondosa			1			75	244	Unintentional introduction, it has been suggested that by waterfowl or with trade (Casasayas, 1989; Sanz-Elorza et al., 2004a). We think an introduction with contaminated goods is more likely. MRT from the literature (Casasayas, 1989).
Bidens pilosa			1			68	15	Unintentional introduction probably linked to trade (Sanz-Elorza et al., 2004a), we think possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Casasayas, 1989).
Bidens subalternans			1			84	222	Probably introduced as a seed contaminant (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Bothriochloa barbinodis				1		10	1	Possibly spread from France by means of rail or road transport (Pyke, 2010). MRT from the literature (Pyke, 2010).
Bougainvillea glabra		1				9	1	Introduced as ornamental (Bolòs et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Boussingaultia cordifolia		1				90	233	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Bouteloua dactyloides		1				5	1	Probably escaped from gardens (Álvarez et al., 2016). MRT from the literature (Álvarez et al., 2016).
Bouteloua gracilis		1				16	1	Origin of the introduction uncertain, possibly through cultivation (Verloove, 2004). MRT from the literature (Verloove, 2004).
Brachiaria platyphylla			1			24	1	Introduced as a seed contaminant (Recasens & Conesa, 1995). MRT from the literature (Recasens & Conesa, 1995).

Brassica juncea		1				90	13	Introduced in Europe through agriculture and as seed contaminant (Casasayas, 1989), an introduction with agriculture is suggested for Spain (Sanz-Elorza et al., 2004a) and adopted here. MRT from the literature (Casasayas, 1989).
Bromus catharticus			1			107	246	Introduced through cultivation in Europe (Casasayas, 1989), but considered unintentional in Catalonia (Casasayas, 1990). Possibly introduced through the textile industry (Casasayas, 1990) or with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Bromus inermis		1	1			37	11	Possibly introduced as a seed contaminant (Casasayas, 1989) and through cultivation (Bolòs et al., 2005). Also recorded as a road verge stabiliser in a neighbouring Spanish region (Esteras, 1988), but we give preference to the work of Casasayas (1989) and Bolòs et al. (2005) because they focused on the study region of the present paper (it can better reflect the regional idiosyncrasies of the study region of Catalonia). MRT from the literature (Soriano, 1984).
Broussonetia papyrifera		1				142	58	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Buddleja davidii		1				58	188	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Campsis radicans		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Canna indica		1				121	53	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cardiospermum halicacabum		1				46	5	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Carpinus betulus	1	1				30	5	Introduced for reforestation and as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Carpobrotus acinaciformis		1				40	8	Introduced through cultivation (Bolòs et al., 2005; Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Carpobrotus edulis		1				107	86	Introduced through cultivation (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Cassia obtusifolia			1			24	1	Introduced as a seed contaminant (Recasens & Conesa, 1995). MRT from the literature (Recasens & Conesa, 1995).

Casuarina cunninghamiana		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Catalpa bignonioides		1				30	7	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cedrus deodara		1				30	2	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cedrus libani subsp. *atlantica*		1				43	5	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cenchrus ciliaris	1					17	4	Probably introduced in neighbouring Spanish region as a road verge stabiliser (Esteras, 1988; Verloove, 2006b). Since in Catalonia it was found in a road interchange (Pyke, 2003) we consider this as a plausible pathway. MRT from the literature (Pyke, 2003).
Cenchrus incertus			1			47	37	Unintentional introduction, probably linked to trade (Sanz-Elorza et al., 2004a). We think it was possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Torrella et al., 1974).
Cephalaria syriaca			1			96	4	Introduced weed (Sanz-Elorza et al., 2004a), we think possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Cadevall, 1923).
Cerastium tomentosum		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Ceratostigma plumbaginoides		1				34	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Cereus peruvianus		1				16	3	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Aymerich & Sáez, 2019b).
Cestrum parqui		1				69	5	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Chamaesyce glomerifera			1			16	1	Origin of the introduction uncertain. In Belgium it has been introduced with imported trees (Verloove, 2005b). Following this previous record, the Catalan introduction may also have originated with imported plants or plant materials, so we assign the contaminant pathway. MRT from the literature (Verloove, 2005b).

Cheiranthus cheiri		1				147	43	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Chenopodium ambrosioides		1				255	297	Introduced through cultivation (Casasayas, 1989; Uotila, 1990). It was considered an unintentional introduction in a more recent review (Sanz-Elorza et al., 2004a), we give preference to earlier works because the focus is on the pathways that first introduced the species. MRT from the literature (Casasayas, 1989).
Chenopodium multifidum			1			117	21	Probably introduced with trade as a contaminant (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Chenopodium pumilio			1			34	33	Introduced with contaminated wool (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Chloris gayana	1					42	22	Introduced as road verge stabiliser (Casasayas, 1989; Esteras, 1988; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Chloris truncata			1			14	1	Origin of the introduction uncertain, it has been recorded in other European countries as a contaminant of wool (Verloove, 2005b), so we assign the contaminant pathway. MRT from the literature (Verloove, 2005b).
Chloris virgata			1			20	1	Unintentional introduction (Sanz-Elorza et al., 2004a), probably as a contaminant. MRT from the literature (Vallverdú, 2000).
Chrysanthemum segetum			1			158	131	Probably introduced as a contaminant of seeds (Casasayas, 1989 MRT from the literature (Casasayas, 1989).
Citrullus colocynthis		1				151	6	Introduced through cultivation (Casasayas, 1989; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Cleome violacea			1			45	2	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Molero, 1976).
Clerodendrum bungei		1				4	1	Introduced as ornamental (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Clerodendrum trichotomum		1				4	1	Introduced as ornamental (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Colocasia esculenta		1				26	2	Inroduced through cultivation (Curcó, 2007). MRT from the literature (Curcó, 2007).
Convolvulus sabatius subsp. *mauritanicus*		1				30	8	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Convolvulus tricolor subsp. *tricolor*		1				107	7	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Font i Quer, 1914).
Conyza bonariensis			1			149	341	Probably introduced with contaminated wool (Casasayas, 1989) or seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Conyza canadensis			1			235	366	Possibly introduced with contaminated cotton (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Conyza sumatrensis			1			115	335	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly as a contaminant. MRT from the literature (Casasayas, 1989).
Coreopsis tinctoria		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Coronilla valentina		1				173	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Coronopus didymus				1		173	150	Probably introduced with ship ballast (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cortaderia selloana		1				35	111	Introduced through cultivation (Casasayas, 1989). It has also been recorded for soil stabilisation, but its use as ornamental was more important (Casasayas, 1989; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Cosmos bipinnatus		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cotoneaster coriaceus		1				21	18	Introduced as ornamental (Aymerich, 2013c). MRT from the literature (Royo, 2006), sub *Cotoneaster lacteus*.
Cotoneaster divaricatus		1				4	1	Escaped from gardens (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Cotoneaster franchetii		1				16	11	Introduced through cultivation (Blanca, 1998). MRT from databases (X. Font, 2019).
Cotoneaster horizontalis		1				6	5	Introduced as ornamental (Aymerich, 2013c). MRT from the literature (Aymerich, 2013c).
Cotoneaster pannosus		1				30	18	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cotoneaster symondsii		1				18	2	Introduced as ornamental (Aymerich, 2001). MRT from the literature (Aymerich, 2001).
Cotula australis			1			45	20	Probably introduced with contaminated wool (Casasayas, 1989). MRT from the literature (Barrau, 1976).

Cotula coronopifolia				1		21	10	Introduced in many countries as ornamental and for revegetation (Brunel et al., 2010), but in Spain it is thought to be an unintentional introduction (Sanz-Elorza et al., 2004a). Unintentional introductions have been linked to ship ballast (Brunel et al., 2010). MRT from databases (X. Font, 2019).
Crassula lycopodioides		1				32	6	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from the literature (Vilar, 1987).
Crataegus azarolus		1				173	4	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Crepis bursifolia			1	1		102	221	Probably introduced with contaminated seeds and with transport (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Crepis sancta subsp. *sancta*			1			149	163	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly as a contaminant. MRT from the literature (Casasayas, 1989).
Cucurbita moschata		1				30	1	Introduced through agriculture (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cupressus arizonica		1				13	1	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Aymerich, 2013c).
Cupressus macrocarpa		1				24	3	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Cuscuta campestris			1			54	243	Probably introduced with contaminated seeds (Casasayas, 1989; Casasayas & Masalles, 1981). MRT from the literature (Casasayas, 1989).
Cylindropuntia imbricata		1				15	5	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from (Sanz-Elorza et al., 2006).
Cylindropuntia pallida		1				9	25	Escaped from gardens (Aymerich, 2015a). MRT from the literature (Aymerich, 2015a).
Cylindropuntia spinosior		1				16	5	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Sanz-Elorza et al., 2004b).
Cymbalaria muralis subsp. *muralis*		1				235	168	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cynara cardunculus		1				136	112	Escaped from cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Cyperus eragrostis				1		82	188	Possibly introduced with ship ballast (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Cyperus imbricatus			1			16	1	Origin of the introduction uncertain (Verloove, 2005b), possibly introduced as wool contaminant and/or an Escape from cultivation (Verloove, 2014). We find more likely an unintentional introduction as a contaminant. MRT from the literature (Verloove, 2005b).
Cyperus papyrus		1				13	1	Introduced as ornamental (Royo, 2006). MRT from the literature (Royo, 2006).
Cyrtomium falcatum		1				37	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Dactyloctenium aegyptium			1			12	1	Probably introduced with contaminated nursery material in an adjacent Spanish region (Aragoneses et al., 2011). We think the contaminant pathway is plausible for the introduction of this species into Catalonia. MRT from the literature (Verloove & Gullón, 2008).
Datura ferox		1	1			173	69	Introduced through cultivation (Casasayas, 1989) and with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Datura innoxia		1	1			153	131	Introduced through cultivation (Casasayas, 1989) and contaminated seeds (Sanz-Elorza et al., 2004a). MRT from the literature (Aymerich & Sáez, 2015).
Datura stramonium		1				173	333	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Datura wrightii		1				36	2	Introduced through cultivation (Aymerich & Sáez, 2015). MRT from the literature (Aymerich & Sáez, 2015).
Delosperma ecklonis		1				4	1	Introduced as ornamental (Aymerich, 2015b). MRT from the literature (Aymerich, 2015b).
Delphinium orientale subsp. *orientale*			1			21	3	Probably introduced with contaminated hay or seeds (Royo, 2006). MRT from databases (X. Font, 2019).
Dichondra micrantha		1				30	7	Introduced through gardening (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Digitaria ciliaris			1			18	4	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly as a contaminant. MRT from the literature (Pyke, 2008).
Digitaria violascens			1			16	3	Lawn weed (Pyke, 2008; Verloove & Gullón, 2008), we think probably introduced with contaminated plant material. MRT from the literature (Pyke, 2008).

Dimorphotheca pluvialis		1				9	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Diospyros lotus		1				173	3	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Diplachne fusca subsp. *uninervia*			1			34	6	Introduced as a seed contaminant (Recasens & Conesa, 1995). MRT from the literature (Recasens & Conesa, 1995).
Dipsacus sativus		1				173	6	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Disphyma crassifolium		1				30	4	Introduced through gardening (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Doxantha unguis-cati		1				30	5	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Drosanthemum floribundum		1				30	6	Introduced through gardening (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Drosanthemum hispidum		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Echinopsis eyriesii		1				4	1	Introduced as ornamental (Aymerich, 2015a). MRT from the literature (Aymerich, 2015a).
Echinopsis schickendantzii		1				4	1	Introduced as ornamental (Aymerich, 2015a). MRT from the literature (Aymerich, 2015a).
Echinopsis spachiana		1				4	2	Introduced as ornamental (Aymerich, 2015a). MRT from the literature (Aymerich, 2015a).
Eclipta prostrata			1			126	67	Introduced weed (Sanz-Elorza et al., 2004a), we think probably as a contaminant. MRT from the literature (Casasayas, 1989).
Ehrharta erecta		1				16	1	We think probably introduced through cultivation. MRT from the literature (Pyke, 2008).
Ehrharta longiflora			1			38	1	Origin of the introduction uncertain (Casasayas, 1989), possibly with contaminated seeds into a botanical garden (Casasayas, 1990). MRT from the literature (Casasayas, 1989).

Einadia nutans			1			48	6	Introduction linked to a botanical garden, probably as a seed or soil contaminant rather than cultivation (Casasayas, 1989) sub *Rhagodia nutans*. MRT from the literature (Casasayas, 1989).
Elaeagnus angustifolia		1				86	86	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Eleusine indica			1			111	145	Possibly introduced with contaminated wool (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Eleusine tristachya subsp. *barcinonensis*			1			142	169	Probably introduced as a wool alien (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Elymus elongatus subsp. *ponticus*	1					14	2	Introduced for road verge stabilisation (Pyke, 2008; Verloove & Gullón, 2008). MRT from the literature (Pyke, 2008).
Epilobium brachycarpum					1	18	1	Probably spread from adjacent Spanish regions (Aymerich, 2013d). MRT from the literature (Aymerich, 2013d).
Eragrostis curvula	1					122	23	Introduced for road verge stabilisation (Verloove, 2003, 2004). MRT from the literature (Casasayas, 1989).
Eragrostis mexicana subsp. *virescens*			1			23	12	Unintentional introduction (Sanz-Elorza et al., 2004a), we think probably as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Eragrostis pectinacea			1			35	1	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly introduced as a contaminant. MRT from the literature (Casasayas, 1989).
Erigeron annuus		1				90	77	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Erigeron karvinskianus		1				102	24	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Eriobotrya japonica		1				104	24	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Eschscholzia californica		1				30	10	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Eucalyptus camaldulensis		1				42	6	Introduced through cultivation for forestry and as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Eucalyptus globulus		1				32	12	Introduced through cultivation for forestry and as ornamental (Casasayas, 1989). It is also used to drain water bodies (Casasayas, 1989), but we think that the ornamental or forestry pathways (both an Escape) are of greater importance. MRT from databases (X. Font, 2019).
Euonymus japonicus		1				30	16	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Euphorbia dentata			1			13	1	Probably introduced with contaminated crops or plant products (Pyke, 2008). MRT from the literature (Pyke, 2008).
Euphorbia glyptosperma			1			4	1	We think possibly introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Aymerich, 2016).
Euphorbia humifusa			1			30	2	Introduced to the West and North of Europe through cultivation in botanical gardens (Casasayas, 1989), but an unintentional introduction is suggested for Spain (Sanz-Elorza et al., 2004a). We think it was possibly introduced as a contaminant. MRT from the literature (Casasayas, 1989).
Euphorbia maculata				1		94	75	Introduced to France with ship ballast, probably introduced into Catalonia by railway transport (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Euphorbia marginata		1				30	6	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Euphorbia nutans			1			111	196	Origin of the introduction uncertain, probably linked to trade (Casasyas 1989). An introduction with contaminated seeds has been suggested (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Euphorbia prostrata			1			107	211	Probably introduced with contaminated seeds (Casasayas, 1989; Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Euphorbia serpens				1		106	71	Introduced with ship ballast in France (Casasayas, 1989), we think this pathway is also plausible for Catalonia. MRT from the literature (Casasayas, 1989).
Fagopyrum esculentum		1				142	14	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Fallopia baldschuanica		1				36	105	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Feijoa sellowiana		1				29	1	Introduced through cultivation (Isern et al., 1984; Paiva, 1997). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Festuca valesiana			1			16	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from (Pyke, 2008), sub *Festuca valesiaca*.
Ficus elastica		1				9	3	Introduced as ornamental (Isern et al., 1984). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Forsythia x intermedia		1				5	1	Introduced through gardening (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Fraxinus ornus		1				39	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Fraxinus pennsylvanica		1				26	2	Introduced as ornamental (Bolòs et al., 2005). MRT from the literature (Balada, 2017).
Freesia refracta		1				30	7	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Gaillardia aristata		1				30	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Galinsoga ciliata			1			37	60	Introduced weed (Sanz-Elorza et al., 2004a), we think probably as a contaminant. MRT from the literature (Casasayas, 1989).
Galinsoga parviflora			1			47	80	Unintentional introduction (Sanz-Elorza et al., 2004a). Possibly introduced with contaminated hay (Folch & Abellà, 1974). Casasayas (1989) argued for multiple introductions, at least partially linked to the cotton trade (cotton-waste was used as field manure). MRT from the literature (Folch & Abellà, 1974).
Gazania linearis		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Gazania rigens		1				32	11	Escaped from gardens (Royo, 2006). MRT from databases (X. Font, 2019).
Gleditsia triacanthos		1				111	105	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Glottiphyllum longum		1				12	1	Introduced as ornamental (Mallol & Maynés, 2006). MRT from the literature (Mallol & Maynés, 2006).
Glycine max		1				6	1	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Gnaphalium purpureum			1			17	2	Introduced as a weed (Sanz-Elorza et al., 2004a), we think probably as contaminant. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Gnaphalium subfalcatum					1	19	11	The first Catalan records were found close to the French border (J. Font et al., 2002), sub *Gamochaeta subfalcata*, we think it is plausible that it has spread into Catalonia unaided. MRT from the literature (J. Font et al., 2002).
Gomphocarpus fruticosus		1				173	121	Introduced through cultivation (Casasayas, 1989). MRT from the literatura Casasayas (1989).
Graptopetalum paraguayense		1				6	1	Introduced as ornamental (Sáez & Guillot, 2014). MRT from the literature (Sáez & Guillot, 2014).
Guizotia abyssinica			1			47	20	Possibly introduced with contaminated soil and gravel used in roadworks, and with birdseed (Casasayas, 1989). This plant was cultivated in Spain, although very rarely (Casasayas, 1989; Folch & Abellà, 1974). It is considered an unintentional introduction in Spain (Sanz-Elorza et al., 2004a), so we only assign the Contaminant pathway. MRT from the literature (Folch & Abellà, 1974).
Gypsophila elegans		1				17	1	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Vigo et al., 2003).
Hedera cf. algeriensis		1				12	2	Introduced through cultivation (Pyke, 2008). MRT from the literature (Pyke, 2008).
Hedera hibernica		1				12	5	Introduced as ornamental (Aymerich, 2013c; Pyke, 2008). MRT from the literature (Pyke, 2008).
Hedera maroccana		1				5	8	Introduced as ornamental (Aymerich & Sáez, 2015). MRT from the literature (Aymerich & Sáez, 2015).
Hedysarum coronarium		1				90	10	Introduced through agriculture (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Helianthus annuus		1				134	57	Introduced through agriculture (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Helianthus tuberosus		1				235	325	Introduced though cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Helianthus x laetiflorus		1				4	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Aymerich, 2016).
Helichrysum orientale		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Heliotropium amplexicaule		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Heliotropium curassavicum				1		114	51	Possibly introduced with ship ballast (Casasayas, 1989; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Hemerocallis fulva		1				86	58	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Heracleum mantegazzianum					1	7	5	Possibly spread from adjacent European countries (Aymerich, 2013d). MRT from (Aymerich, 2013d).
Hesperis matronalis subsp. *matronalis*		1				26	6	Introduced as ornamental (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Hibiscus trionum			1			142	11	Unintentional introduction (Sanz-Elorza et al., 2004a), we think probably as a contaminant. MRT from the literature (Casasayas, 1989).
Hordeum distichon		1				30	9	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Hypericum calycinum		1				30	2	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Impatiens balfourii		1				43	123	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Impatiens balsamina		1				134	2	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Impatiens glandulifera					1	9	29	Introduced through cultivation in the South of France (Bolòs & Vigo, 1996; Casasayas, 1989), from where it probably has spread into Catalonia (Aymerich, 2016; Rifà, 2015). MRT from the literature (Rifà, 2015).
Inula helenium		1				100	92	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Ipomoea hederacea			1			24	1	Introduced as a seed contaminant (Recasens & Conesa, 1995). MRT from the literature (Recasens & Conesa, 1995).
Ipomoea indica		1				30	189	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Ipomoea purpurea		1				69	242	Introduced through cultivation (Casasayas, 1989). MRT from databases (X. Font, 2019).
Ipomoea sagittata					1	51	23	Introduced to Europe through cultivation (Sanz-Elorza et al., 2004a), and probably also with ship ballast (Austin, 2014). It was first reported in Spain in the adjacent

								region of Valencia, and it has been suggested that the species might spread via seeds drifting in sea water (Austin, 2014). In Catalonia it has been reported in the Ebro delta, since we don't find bibliographic evidence of cultivation (Bolòs et al., 2005; Bolòs & Vigo, 1996; Curcó, 2007; Royo, 2006), we think an unaided spread from Valencia is possible. MRT from databases (X. Font, 2019).
Ipomoea violacea		1				2	1	Probably introduced as ornamental, like it has been suggested in an adjacent Spanish region (Guillot & Van der Meer, 2004). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Iris albicans		1				12	7	Introduced as ornamental (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Jasminum nudiflorum		1				102	2	Introduced as ornamental (Bolòs et al., 2005). MRT from the literature (Casasayas, 1989).
Jasminum officinale		1				235	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Juglans nigra		1				116	1	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Juncus tenuis		1				99	60	Unintentional introduction (Sanz-Elorza et al., 2004a), we think probably as a contaminant. MRT from the literature (Casasayas, 1989).
Kalanchoe daigremontiana		1				12	6	Introduced as ornamental (Pyke, 2008). MRT from the literature (Pyke, 2008).
Kalanchoe x houghtonii		1				16	10	Introduced through cultivation (Mesquida et al., 2017). MRT from the literature (Mesquida et al., 2017).
Kochia scoparia		1				142	208	Introduced through cultivation (Casasayas, 1989). MRT from Casasayas (1989).
Koelreuteria paniculata		1				30	5	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Laburnum anagyroides		1				142	5	Introduced as ornamental (Casasayas, 1989 MRT from the literature (Casasayas, 1989).
Lampranthus multiradiatus		1				17	1	Introduced as ornamental (Aymerich, 2015c). MRT from the literature (Royo, 2006).
Lantana camara		1				30	15	Introduced as ornamental (Bolòs et al., 2005). MRT from the literature (Casasayas, 1989).
Lantana montevidensis		1				30	2	Introduced as ornamental (Casasayas, 1989). MRT from Casasayas (1989)
Larix decidua		1				33	4	Introduced for forestry (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Lathyrus odoratus		1				69	2	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Lathyrus tingitanus		1				88	27	Introduced through agriculture (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Lavandula dentata		1				173	12	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Leonitis leonorus		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from Casasayas (1989)
Leonurus cardiaca		1				106	8	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Lepidium bonariense			1			42	3	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly with contaminated wool (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Lepidium densiflorum			1			7	1	Origin of the introduction uncertain (Pyke, 2013). We think it was possibly introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Pyke, 2013).
Lepidium latifolium subsp. *latifolium*		1				28	1	Introduced through cultivation (Royo, 2006). MRT from databases (X. Font, 2019).
Lepidium perfoliatum			1			69	3	Unintentional introduction (Sanz-Elorza et al., 2004a). We think it was possibly introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Casasayas, 1989).
Lepidium virginicum subsp. *virginicum*					1	90	72	Introduced into France with ship ballast. Populations have established in the South of France (Casasayas, 1989), some very close to the border (Bolòs & Vigo, 1990). Given the location of some of the earliest Catalan records, we think an unaided spread into Catalonia is plausible. MRT from the literature (Casasayas, 1989).
Leucaena leucocephala		1				30	4	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Levisticum officinale subsp. *officinale*		1				106	1	Introduced through agriculture (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Ligustrum lucidum		1				26	30	Introduced as ornamental (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Ligustrum ovalifolium		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Linaria spartea				1		33	1	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Lippia filiformis		1				102	118	Introduced through cultivation (Casasayas, 1989) sub *Lippia canescens*. MRT from the literature (Casasayas, 1989).
Lonicera japonica		1				58	252	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Lunaria annua subsp. *annua*		1				173	91	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Lupinus polyphyllus		1				27	8	Introduced as ornamental (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Lycium barbarum		1				9	1	Introduced through gardening (Bolòs et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Lycium chinense		1				69	3	Introduced as ornamental (Bolòs et al., 2005). MRT from the literature (Casasayas, 1989).
Mahonia aquifolium		1				30	7	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Malephora crocea		1				12	1	Introduced as ornamental (Pyke, 2008). MRT from the literature (Pyke, 2008).
Malope trifida		1				21	1	Introduced as ornamental (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Matthiola lunata			1			16	1	Introduction probably linked to re-sowing of road verges (Vigo et al., 2003), probably as a contaminant. MRT from the literature (Vigo et al., 2003).
Megathyrsus maximus	1					16	1	Probably introduced as a road verge stabiliser (Verloove, 2006b). MRT from the literature (Verloove, 2005b), sub *Urochloa maxima*.
Melia azedarach		1				74	15	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Mesembryanthemum crystallinum		1				69	7	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Mimulus guttatus		1				15	1	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Mirabilis jalapa		1				134	182	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Modiola caroliniana			1			27	1	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Muhlenbergia schreberi			1			87	1	Found in plantations of *Platanus* and *Populus* (Pyke, 2008), we think most likely as a contaminant. MRT from the literature (Pyke, 2008).
Myoporum laetum		1				13	11	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Nassella tenuissima		1				6	1	Introduced as ornamental (Álvarez et al., 2016; Verloove, 2005a). MRT from the literature (Álvarez et al., 2016).
Nepeta cataria		1				87	86	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Nephrolepis cordifolia		1				12	1	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Pyke, 2008)
Nicandra physalodes		1				140	1	Introduced as ornamental (Casasayas, 1989). MRT from Casasayas (1989)
Nicotiana glauca		1				111	102	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Nicotiana tabacum		1				140	1	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Nothoscordum borbonicum		1				111	29	Introduced as ornamental (Casasayas, 1989) sub *Nothoscordum inodorum*. MRT from the literature (Casasayas, 1989).
Oenothera biennis subsp. *biennis*		1				171	90	Introduced through cultivation (Casasayas, 1989) sub *Oenothera biennis*. MRT from the literature (Sanz-Elorza et al., 2004a).
Oenothera biennis subsp. *suaveolens*		1				95	34	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Casasayas, 1989) sub *Oenothera suaveolens*.
Oenothera glazioviana		1				111	95	Introduced through cultivation (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989) sub *Oenothera erytrosepala*.
Oenothera indecora subsp. *indecora*		1				14	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Verloove & Gullón, 2008).
Oenothera rosea			1			142	108	Possibly introduced through botanical gardens (Casasayas, 1989). We think an unintentional introduction is plausible (Oliver, 2009), like it has been suggested in an

								adjacent Spanish region (Sanz-Elorza et al., 2011) and in Belgium (Verloove, 2006a). MRT from the literature (Casasayas, 1989).
Oenothera speciosa		1				6	2	Introduced as ornamental (Álvarez et al., 2016; Dietrich, 1997). MRT from the literature (Álvarez et al., 2016).
Ononis mitissima					1	12	1	Origin of the introduction uncertain, we think possibly spread from adjacent Spanish regions. MRT from the literature (Pyke, 2009).
Opuntia ammophila		1				9	2	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Opuntia auberi		1				16	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Sanz-Elorza et al., 2004a).
Opuntia aurantiaca		1				8	1	Introduced as ornamental (Guàrdia, 2016). MRT from the literature (Guàrdia, 2016).
Opuntia engelmannii		1				16	7	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Sanz-Elorza et al., 2004b).
Opuntia ficus-indica		1				235	197	Introduced through cultivation (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Opuntia huajuapensis		1				16	2	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Opuntia humifusa		1				29	17	Introduced through cultivation (Bolòs et al., 2005) sub *Opuntia vulgaris*. MRT from the literature (Gómez-Bellver & Sáez, 2017).
Opuntia leucotricha		1				5	3	Introduced as ornamental (Sáez et al., 2015). MRT from the literature (Sáez et al., 2015).
Opuntia lindheimeri		1				15	8	Introduced through gardening (Sanz-Elorza et al., 2004a), sub *Opuntia lindheimeri* var. *linguliformis*. MRT from the literature (Sanz-Elorza et al., 2004a), sub *Opuntia lindheimeri* var. *linguliformis*.
Opuntia microdasys		1				15	5	Introduced through cultivation (Aymerich, 2015a). MRT from the literature (Sanz-Elorza et al., 2004b).
Opuntia monacantha		1				16	4	Introduced through cultivation (Sanz-Elorza et al., 2004a). MRT from the literature (Sanz-Elorza et al., 2004a).
Opuntia phaeacantha		1				4	3	Introduced as ornamental (Aymerich, 2015a). MRT from the literature (Aymerich, 2015a).

Opuntia scheeri		1				4	3	Introduced as ornamental (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Opuntia schickendantzii		1				5	2	Introduced as ornamental (Aymerich, 2015a). MRT from the literature (Aymerich, 2015a).
Opuntia stricta		1				29	22	Introduced through cultivation (Bolòs et al., 2005). MRT from Sanz-Elorza et al. (2004b).
Opuntia subulata		1				30	35	Introduced through cultivation (Casasayas, 1989) sub *Austrocylindropuntia subulata*. MRT from the literature (Casasayas, 1989).
Opuntia tomentosa		1				4	1	Introduced as ornamental (Aymerich, 2015b). MRT from the literature (Aymerich, 2015b).
Opuntia tuna		1				16	3	Introduced as ornamental (Aymerich, 2015a). MRT from the literature (Royo, 2006).
Ornithogalum arabicum		1				158	7	Although considered an accidental introduction by Casasayas (1989), we find it more likely to be introduced through cultivation (Bolòs & Vigo, 2001; Martínez-Azorín et al., 2013). MRT from the literature (Casasayas, 1989).
Oxalis articulata		1				102	178	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Oxalis bowiei		1				30	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Oxalis debilis subsp. *corymbosa*		1	1			93	111	Possibly introduced as ornamental (Casasayas, 1989) sub *Oxalis latifolia*, also reported as a probable seed contaminant (Masalles et al., 1996). MRT from the literature (Casasayas, 1989) sub *Oxalis latifolia*.
Oxalis dillenii		1				9	2	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Aymerich, 2013a).
Oxalis latifolia		1	1			117	198	Possibly introduced through cultivation (Casasayas, 1989) and as a contaminant of seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Oxalis pes-caprae		1	1			116	99	Introduced through cultivation and as a contaminant (Casasayas, 1989; Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Panicum antidotale			1			34	16	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly with contaminated seeds. MRT from the literature (Benedí et al., 1986).
Panicum capillare		1	1			99	129	Introduced as ornamental (Bolòs et al., 2005; Casasayas, 1989) and as a seed contaminant (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).

Panicum dichotomiflorum			1			37	80	Probably introduced with contaminated seeds (Casasayas, 1989; Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Panicum philadelphicum subsp. *gattingeri*			1			14	1	Weed of maize in Italy and Slovenia (Verloove & Gullón, 2008), so we think it has possibly been introduced with contaminated seeds. MRT from the literature (Verloove & Gullón, 2008).
Parkinsonia aculeata		1				30	8	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Parthenocissus quinquefolia		1				43	71	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Parthenocissus tricuspidata		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Pascalia glauca			1			2	1	Unintentional introduction (Sanz-Elorza et al., 2004a), sub *Wedelia glauca*, we think possibly introduced as a contaminant. MRT from the literature (S. Argemí & Izuzquiza, 2017), sub *Wedelia glauca*.
Paspalum dilatatum		1	1			112	197	Introduced through cultivation and as a contaminant (Casasayas, 1989; Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Paspalum distichum			1			111	253	Probably introduced with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Paspalum saurae		1	1			22	6	Introduced through cultivation (Greuter & Raus, 2004), sub *Paspalum notatum*, and as a weed of lawns (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Paspalum vaginatum			1			112	35	Possibly introduced as a seed contaminant (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Passiflora caerulea		1				30	11	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Pelargonium peltatum		1				30	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Pennisetum clandestinum		1				13	7	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Pyke, 2008)
Pennisetum setaceum		1				21	4	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Pennisetum villosum		1				115	27	Introduced as ornamental (Casasayas, 1989). Also recorded as a road verge stabiliser in a neighbouring Spanish region (Esteras, 1988), but since only the ornamental pathway is mentioned in Casasayas (1989) we assign only the Escape pathway. We give preference to the work of Casasayas (1989) because it focused on the study region of the present paper (it can better reflect the regional idiosyncrasies of the study region of Catalonia). MRT from the literature (Casasayas, 1989).
Perilla frutescens		1				30	2	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Periploca graeca		1				30	4	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Persicaria capitata		1				4	1	Introduced through gardening (Sáez & Guillot, 2015). MRT from the literature (Sáez & Guillot, 2015).
Phacelia tanacetifolia		1				25	3	Introduced through cultivation (Álvarez et al., 2016). MRT from the literature (Sáez et al., 2000).
Phalaris canariensis subsp. *canariensis*		1				150	103	Introduced through cultivation (Casasayas, 1989) sub *Phalaris canariensis*. MRT from the literature (Casasayas, 1989).
Phalaris stenoptera	1					16	6	Probably introduced as a road verge stabiliser in a neighbouring Spanish region (Esteras, 1988) sub *Phalaris aquatica* var. *stenoptera*. We think this is a plausible pathway as it is commonly found near roads (Álvarez et al., 2016; Pyke, 2008). MRT from the literature (Pyke, 2008)
Phedimus spurius		1				27	3	Escaped from gardens (Aymerich, 2017). MRT from the literature (Aymerich, 2017).
Philadelphus coronarius		1				173	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Phlomis fruticosa		1				87	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Phlomis purpurea subsp. *purpurea*		1				87	2	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Phoenix canariensis		1				30	20	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Phyllostachys aurea		1				16	7	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).

Physalis fusco-maculata			1			30	2	Introduced in Europe as a wool contaminant (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Physalis ixocarpa		1				17	2	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Verloove, 2003).
Physalis peruviana		1				142	2	Introduced through agriculture (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Physalis philadelphica		1				33	3	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Phytolacca americana		1				173	171	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Phytolacca dioica		1				24	5	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Picea abies subsp. *abies*		1				53	17	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Vigo, 1976).
Pinus radiata		1				69	31	Introduced for forestry (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Pinus wallichiana		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Pistacia vera		1				96	1	Introduced through agriculture (Sanz-Elorza et al., 2004a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Pittosporum heterophyllum		1				9	2	Introduced as ornamental (Isern et al., 1984). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Pittosporum tobira		1				30	30	Escaped from cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Platanus Xhispanica		1				86	280	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Plumbago auriculata		1				30	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Podranea ricasoliana		1				14	2	Escaped from gardens (Mallol & Maynés, 2008). MRT from the literature (Mallol & Maynés, 2008).

Polygonum orientale		1				35	12	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Populus canescens	1	1				16	2	Probably introduced through cultivation (Bolòs et al., 2005) and slope stabilisation (Aymerich, 2016). MRT from databases (X. Font, 2019).
Populus deltoides		1				55	52	Introduced through cultivation for forestry and as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Populus Xcanadensis		1				142	112	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Portulaca grandiflora		1				30	8	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Potentilla norvegica			1			7	1	Origin of the introduction uncertain. Possibly introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Prunus cerasifera		1				43	12	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Prunus laurocerasus		1				104	8	Introduced as ornamental (Bolòs et al., 2005). MRT from the literature (Casasayas, 1989).
Pseudotsuga menziesii	1	1				34	4	Introduced for forestry (Sanz-Elorza et al., 2004a) and for reforestation (Oliver, 2009). MRT from the literature (Broncano et al., 2005).
Pteris vittata		1				69	1	Introduced through cultivation (Verloove & Gullón, 2008). MRT from databases (X. Font, 2019).
Puccinellia distans					1	34	1	Origin of the introduction uncertain, we think it was possibly introduced by waterfowl. MRT from databases (X. Font, 2019).
Pyracantha angustifolia		1				21	10	Introduced through cultivation (Bolòs et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Pyracantha crenatoserrata		1				11	2	Introduced through cultivation (Bolòs et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Pyracantha crenulata		1				30	3	Introduced through gardening (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Pyracantha fortuneana		1				6	2	Introduced as ornamental (Aymerich, 2013c). MRT from the literature (Aymerich, 2013c).

Quercus rubra	1					35	2	Introduced through gardening and for reforestation (Oliver, 2009). We think that its use for reforestation has played a bigger role in its establishment than its use as ornamental, so we assign the release pathway. MRT from databases (X. Font, 2019).
Retama monosperma		1				30	6	Introduced as ornamental (Casasayas, 1989) sub *Lygos monosperma*. MRT from the literature (Casasayas, 1989) sub *Lygos monosperma*.
Reynoutria japonica		1			1	45	13	Introduced as ornamental (Casasayas, 1989), although the species was first recorded close to the French border, so we think it is plausible that it also spread from France. MRT from the literature (Casasayas, 1989).
Rhaponticum repens			1			10	1	Probably introduced in the USA with contaminated seeds (López-Alvarado et al., 2011). We think the contaminant pathway is also likely for the Catalan population. MRT from the literature (López-Alvarado et al., 2011).
Rhus coriaria		1				69	6	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Rhus typhina		1				6	1	Introduced as ornamental (Aymerich, 2014). MRT from the literature (Aymerich, 2014).
Ribes rubrum		1				155	11	Introduced through agriculture (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Robinia pseudoacacia		1				147	349	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Rosa moschata		1				104	6	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Rubia tinctorum		1				142	115	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Rumex cristatus				1		23	28	This species is spreading in Spain (Pino, 1998; Verloove & Gullón, 2008), we think probably as a stowaway. MRT from the literature (Pino, 1998)
Ruta graveolens		1				139	3	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Salix babylonica		1				55	12	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Salix pentandra					1	74	1	Origin of the introduction uncertain, possibly escaped from cultivation or spread from France (Pedrol, 2017). We think unaided spread is more likely given the proximity to the French border. MRT from databases (X. Font, 2019).
Salix Xrubens		1				86	56	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Salpichroa origanifolia		1				69	4	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Salvia fruticosa		1				117	1	Introduced as ornamental (Sáez, 2010). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Salvia microphylla		1				90	2	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Salvia verticillata		1				74	18	Introduced as ornamental (Guardiola et al., 2009). MRT from databases (X. Font, 2019).
Satureja hortensis		1				87	5	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Saxifraga stolonifera		1				22	1	Introduced through gardening (M. Campos & Fàbregas, 1999). MRT from the literature (M. Campos & Fàbregas, 1999).
Schinus molle		1				117	12	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from the litearture (Sanz-Elorza et al., 2004a).
Schkuhria pinnata			1			23	2	Unintentional introduction (Sanz-Elorza et al., 2004a), possibly as a contaminant of seeds or grain, like it has been suggested in an adjacent Spanish region (Calduch, 1961) MRT from the literature (Bolòs & Vigo, 1996).
Scilla peruviana		1				152	3	Introduced as ornamental (Bolòs et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Secale cereale		1				100	51	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Sedum dendroideum		1				90	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Sedum rubrotinctum		1				30	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Sedum sarmentosum		1				27	1	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Castroviejo & Velayos, 1995).
Senecio angulatus		1				30	25	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Senecio deltoideus		1				30	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Casasayas, 1989).
Senecio inaequidens					1	34	195	Probably spread from France (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Senecio macroglossus		1				30	14	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Senecio mikanioides		1				30	34	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Senecio pseudolongifolius		1				30	3	Introduced as ornamental (Casasayas, 1989) sub *Senecio lineatus*. MRT from the literature (Casasayas, 1989) sub *Senecio lineatus*.
Senecio pterophorus			1			37	34	Possibly introduced with contaminated wool (Verloove, 2005b). MRT from the literature (Chamorro et al., 2006).
Senecio tamoides		1				16	7	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from databases (X. Font, 2019).
Sesbania exaltata			1			24	1	Introduced as a seed contaminant (Recasens & Conesa, 1995). Although it is sometimes cultivated, its presence in Catalonia is most likely unintentional (Recasens & Conesa, 1995; Sanz-Elorza et al., 2004a). MRT from the literature (Recasens & Conesa, 1995).
Setaria faberi			1			24	2	Introduced as a seed contaminant (Recasens & Conesa, 1995). MRT from the literature (Recasens & Conesa, 1995).
Setaria parviflora				1		45	125	Origin of the introduction uncertain, probably related to trade (Casasayas, 1990), we think possibly as a contaminant. MRT from the literature (Casasayas, 1989) sub *Setaria geniculata*.
Sicyos angulatus			1			23	5	Introduced to Europe as ornamental in the 19th century, and more recently as a contaminant (Brunel et al., 2010). The first Catalan record is from 1996, and we don't find evidence of cultivation (Fàbregas et al., 1996), so an unintentional introduction as a contaminant is more likely. MRT from the literature (Fàbregas et al., 1996).

Sida rhombifolia		1				24	2	Introduced through cultivation (Curcó, 2007). MRT from the literature (Curcó, 2007).
Sida spinosa			1			33	20	Introduced as a seed contaminant (Recasens & Conesa, 1995). MRT from the literature (Mayoral, 1987).
Silene cretica			1			137	3	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from databases (X. Font, 2019).
Silene dichotoma			1			43	5	Probably introduced as a seed contaminant (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Silene pseudoatocion		1				31	1	Introduced as ornamental (Royo, 2006). MRT from databases (X. Font, 2019).
Sisyrinchium platense		1				35	4	Origin of the introduction uncertain (Conesa, 1991), we think possibly introduced as ornamental. MRT from the literature (Conesa, 1991).
Solanum bonariense					1	107	17	Probably spread from France (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Solanum chenopodioides			1			58	143	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly as a contaminant. MRT from the literature (Casasayas, 1989).
Solanum chrysotrichum			1			15	1	We think possibly introduced as a contaminant. MRT from the literature (Mallol & Maynés, 2008).
Solanum elaeagnifolium			1			35	42	Introduced as a contaminant (Brunel et al., 2010). MRT from the literature (Casasayas, 1989).
Solanum laciniatum		1				39	1	Possibly introduced as ornamental (Casasayas, 1989) or through agriculture (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Solanum linnaeanum		1				173	22	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Solanum mauritianum		1				4	1	Introduced as ornamental (Sanz-Elorza et al., 2004a). MRT from the literature (Aymerich, 2015b).
Solanum physalifolium			1			6	1	Unintentional introduction (Sanz-Elorza et al., 2004a), mostly associated with crops (Sobrino & Sanz-Elorza, 2012). We think it has been probably been introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from the literature (Aymerich, 2014).
Solanum pseudocapsicum		1				30	6	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Solanum rostratum			1			107	39	In its native range (Mexico and South-West United States of America), its fruits (covered with hooked spikes) attach to the fur of animals (Casasayas, 1989). We think it might have been introduced with contaminated animal products. MRT from the literature (Casasayas, 1989).
Solanum sisymbrifolium			1			14	1	Unintentional introduction (Sanz-Elorza et al., 2004a), we think most likely as a contaminant. MRT from the literature (Gómez-Bellver et al., 2016).
Solanum tuberosum		1				87	230	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Soleirolia soleirolii		1				30	8	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Solidago canadensis subsp. *altissima*		1				35	21	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Solidago canadensis subsp. *canadensis*		1				100	173	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Solidago gigantea subsp. *serotina*		1				43	5	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Soliva sessilis			1			8	2	Probably introduced as a seed contaminant (Vilar et al., 2018). MRT from the literature (Pyke, 2013).
Spartina versicolor				1		102	19	Origin of the introduction uncertain, probably linked to its former use as packaging material for maritime trade (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Spiraea cantoniensis		1				36	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Sporobolus indicus		1				166	208	Probably introduced through gardening (Casasayas, 1989). It was considered an introduced weed in a more recent review (Sanz-Elorza et al., 2004a), we give preference to the work of Casasayas (1989) because it focused on the study region of the present paper (it can better reflect the regional idiosyncrasies of the study region of Catalonia). MRT from the literature (Casasayas, 1989).
Stachys byzantina		1				142	90	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Stenotaphrum secundatum		1				38	57	Introduced through gardening (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Stipa brachychaeta			1			18	2	Unintentional introduction (Verloove, 2005a), sub *Jarava brachychaeta*, we think possibly as a contaminant. MRT from the literature (Verloove, 2005a), sub *Jarava brachychaeta*.
Stipa mucronata		1				19	2	Origin of the introduction uncertain (J. Font et al., 2001), sub *Nassella mucronata*. We think it was possibly introduced through gardening or agriculture. MRT from (J. Font et al., 2001), sub *Nassella mucronata*.
Stipa neesiana				1		48	7	Possibly introduced into France with contaminated wool and railway traffic (Verloove, 2005a). The first Catalan localities were reported near the border (J. Font et al., 2001; Pyke, 2008), so we think a spread from France by means of rail or road transport is plausible. MRT from the literature (Pyke, 2008).
Stipa papposa			1			34	4	Probably introduced as a contaminant of wool (Casasayas, 1989; Verloove, 2005a), sub *Jarava plumosa*. MRT form Casasayas (1989).
Stipa trichotoma			1			33	4	Probably introduced with wool (Verloove, 2005a), sub *Nassella trichotoma*. MRT from the literature (Carreras et al., 1991).
Symphoricarpos albus		1				7	2	Introduced as ornamental (Aymerich, 2013d). MRT from the literature (Aymerich, 2013d).
Tagetes minuta			1			93	193	Unintentional introduction (Sanz-Elorza et al., 2004a), probably introduced as a wool or seed contaminant (Casasayas, 1989; Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Tagetes patula		1				30	5	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Tanacetum balsamita		1				43	70	Introduced through cultivation (Bolòs et al., 2005). MRT from databases (X. Font, 2019).
Tanacetum cinerariifolium		1				69	29	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Tecomaria capensis		1				11	2	Introduced through gardening (Mallol & Maynés, 2008). MRT from the literature (Mallol & Maynés, 2008).
Teucrium fruticans		1				69	11	Introduced as ornamental (Bolòs et al., 2005). MRT from databases (X. Font, 2019).

Thuja orientalis		1				36	2	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Tilia tomentosa		1				6	1	Introduced as ornamental (Aymerich, 2013c). MRT from the literature (Aymerich, 2013c).
Tipuana tipu		1				9	2	Introduced as ornamental (Bolòs et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Trachycarpus fortunei		1				13	5	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Tradescantia fluminensis		1				42	45	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Tradescantia pallida		1				4	1	Introduced as ornamental (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Tradescantia zebrina		1				4	1	Introduced as ornamental (Aymerich, 2016). MRT from the literature (Aymerich, 2016).
Trichloris crinita			1			8	1	Possibly introduced with contaminated commodities (Álvarez et al., 2016). MRT from the literature (Álvarez et al., 2016).
Trifolium resupinatum			1			137	7	Origin of the introduction uncertain. Possibly introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a). MRT from databases (X. Font, 2019).
Triticum durum		1				30	4	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Tritonia Xcrocosmiflora		1				35	11	Introduced as ornamental (Casasayas, 1989), sub Crocosmia x crocosmiifolia. MRT from the literature (Casasayas, 1989), sub *Crocosmia x crocosmiifolia*.
Tropaeolum majus		1				32	11	Introduced as ornamental (Casasayas, 1989). MRT from databases (X. Font, 2019).
Ulex europaeus			1			40	1	Possibly an unintentional introduction (Casasayas, 1989), we think possibly as a contaminant. MRT from the literature (Casasayas, 1989).
Ulmus pumila		1				30	10	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Ursinia nana subsp. *nana*			1			13	1	Origin of the introduction uncertain (Molero, 2009), we think possibly as a contaminant. MRT from the literature (Molero, 2009).

Verbena bonariensis			1			35	4	Origin of the introduction uncertain (Conesa, 1991), regarded as unintentional in Spain (Sanz-Elorza et al., 2004a). We think it was possibly introduced as a contaminant. MRT from the literature (Conesa, 1991).
Verbena brasiliensis			1			16	1	Possibly introduced as a contaminant, like it has been suggested in Belgium (Verloove, 2006a), sub *Verbena litoralis* var. b*rasiliensis*. MRT from the literature (Álvarez et al., 2016).
Verbena incompta			1			7	1	Unintentional introduction, probably with trade (Verloove, 2011). MRT from the literature (Álvarez et al., 2016).
Verbena litoralis			1			23	5	In Italy this species has occurred after roadworks (Verloove, 2003), so we think it is possibly introduced with contaminated soil or gravel. MRT from the literature (C. Gutiérrez & Sáez, 1996).
Veronica longifolia		1				43	1	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Veronica peregrina subsp. *peregrina*			1			74	10	Its cultivation in botanical gardens played an important role in spreading this species across Europe (Casasayas, 1989), but we think it is more likely that it was introduced in Catalonia and Spain unintentionally with trade (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Viscaria vulgaris		1				10	1	Introduced through cultivation (Aymerich, 2013d). MRT from the literature (Aymerich, 2013d).
Vitis labrusca		1				27	1	Introduced through agriculture (Aymerich, 2013a). MRT from the literature (Aymerich, 2014).
Vitis riparia		1				7	8	Introduced through agriculture (Aymerich, 2013d). MRT from the literature (Aymerich, 2013d).
Vitis rupestris		1				15	15	Introduced through agriculture (Aymerich, 2013a). MRT from the literature (Aymerich, 2014).
Washingtonia filifera		1				30	6	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Washingtonia robusta		1				30	4	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Wigandia caracasana		1				30	3	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

Wisteria sinensis		1				30	4	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Xanthium echinatum subsp. *italicum*			1			102	336	Probably introduced with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989), sub *Xanthium italicum*.
Xanthium orientale			1			142	109	Probably introduced with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Xanthium spinosum			1			173	340	Probably an unintentional introduction linked to the wool trade (Casasayas, 1989; Sanz-Elorza et al., 2004a). It is also recorded as cultivated in botanical gardens, but an introduction with wool seems more likely (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Yucca aloifolia		1				30	5	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Aymerich, 2015d).
Yucca gigantea		1				5	6	Introduced as ornamental (López-Pujol & Guillot, 2014). MRT from the literature (López-Pujol & Guillot, 2014).
Yucca gloriosa		1				30	16	Introduced as ornamental (Aymerich & Gustamante, 2015). MRT from the literature (Aymerich, 2015d).
Yucca recurvifolia		1				30	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Zantedeschia aethiopica		1				43	7	Escaped from cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Zea mays		1				100	41	Introduced through cultivation (Casasayas, 1989). MRT from the literature (Casasayas, 1989).

(e) Plants: aquatic plants (N = 27 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Ammannia baccifera subsp. aegyptiaca			1			67	4	Weed of rice (Casasayas, 1989) sub *Ammania aegyptiaca*, probably introduced as a contaminant of seeds. MRT from the literature (Casasayas, 1989) sub *Ammania aegyptiaca*.

Ammannia coccinea			1			69	70	Probably introduced as a seed contaminant (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Ammannia robusta			1			68	55	Probably introduced as a seed contaminant (Casasayas, 1989; Masalles et al., 1996). MRT from Masalles et al. (1996).
Azolla filiculoides			1		1	68	29	Possibly introduced by waterfowl or contaminated seeds (Casasayas, 1989; Sanz-Elorza et al., 2004a), sub *Azolla caroliniana*. MRT from the literature (Sáez, 1997).
Bergia capensis			1			64	33	Weed of rice (Casasayas, 1989), we think possibly introduced as contaminant. MRT from the literature (Casasayas, 1989).
Cyperus alternifolius subsp. *flabelliformis*		1				47	37	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Echinochloa colona			1			158	173	Unintentional introduction (Casasayas, 1989; Sanz-Elorza et al., 2004a), sub *Echinochloa colonum*, we think probably as a contaminant. MRT from the literature (Casasayas, 1989), sub *Echinochloa colonum*.
Echinochloa crus-galli subsp. *crus-galli*			1			64	149	Introduced weed (Sanz-Elorza et al., 2004a), we think probably as a contaminant (like other species of the same genus included in the present paper). MRT from databases (X. Font, 2019).
Echinochloa crus-galli subsp. *hispidula*			1			31	7	Weed of rice (Casasayas, 1989), sub *Echinochloa hispidula*, probably introduced as a contaminant of seeds (Sanz-Elorza et al., 2004a), sub *Echinochloa hispidula*. MRT from the literature (Casasayas, 1989), sub *Echinochloa hispidula*.
Echinochloa crus-galli subsp. *oryzicola*			1			38	11	Weed of rice (Casasayas, 1989), sub *Echinochloa oryzicola*, probably introduced as a contaminant of seeds (Sanz-Elorza et al., 2004a), sub *Echinochloa oryzicola*. MRT from the literature (Casasayas, 1989), sub *Echinochloa oryzicola*.
Echinochloa crus-galli subsp. *oryzoides*						64	22	Weed of rice (Casasayas, 1989), sub *Echinochloa oryzoides*, probably introduced as a contaminant of seeds (Sanz-Elorza et al., 2004a), sub *Echinochloa oryzoides*. MRT from the literature (Casasayas, 1989), sub *Echinochloa oryzoides*.
Echinochloa telmatophila						3	1	We think it was possibly introduced as a contaminant (like other species of the same genus included in the present paper). MRT from the

								EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Egeria densa		1				23	6	Introduced as ornamental (Aymerich, 2012; Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Eichhornia crassipes		1				21	16	Introduced as ornamental (Royo, 2006; Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Eleocharis bonariensis			1			28	2	Unintentional introduction (Sanz-Elorza et al., 2004a), we think probably as a contaminant. MRT from the literature (Bolòs & Vigo, 2001).
Elodea canadensis		1				114	20	Introduced as ornamental (Casasayas, 1989; Sanz-Elorza et al., 2004a). Other pathways have been suggested (e.g., through the timber trade), but an introduction as ornamental seems more likely (Sanz-Elorza et al., 2004a). MRT from the literature (Casasayas, 1989).
Heteranthera limosa			1			29	5	Introduced as a weed (Sanz-Elorza et al., 2004a), probably introduced as a contaminant. MRT from the literature (Curcó, 2007).
Heteranthera reniformis			1			21	6	Probably introduced with contaminated seeds (Vilar et al., 2018). MRT from databases (X. Font, 2019).
Lemna minuta					1	8	6	Probably introduced by waterfowl (Aymerich, 2013b). MRT from the literature (Aymerich, 2013b).
Lindernia dubia			1			64	63	Probably introduced with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Ludwigia peploides subsp. montevidensis	1	1				63	17	Multiple species in this genus introduced as ornamentals and released to improve fishery in the wild (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Verloove & Gullón, 2008).
Myriophyllum aquaticum		1				30	3	Introduced as ornamental (Casasayas, 1989). MRT from the literature (Casasayas, 1989).
Najas gracillima			1		1	37	28	Possibly introduced by waterfowl (Casasayas, 1989, 1990) or with contaminated seeds (Masalles et al., 1996). MRT from the literature (Casasayas, 1989).
Sagittaria montevidensis subsp. calycina			1			14	1	Weed of rice (Sanz-Elorza et al., 2004a), we think probably introduced as a contaminant. MRT from the literature (Curcó, 2006).

Salvinia natans		1				137	7	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).
Typha laxmannii					1	11	3	Unintentional introduction (Sanz-Elorza et al., 2004a), we think possibly by waterfowl. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Vallisneria spiralis		1				26	3	Introduced through gardening (Sanz-Elorza et al., 2004a). MRT from databases (X. Font, 2019).

(f) Terrestrial invertebrates (N = 100 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Acalyptris platani			1			27	4	Pest of trees (van Nieukerken et al., 2004). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the literature (van Nieukerken et al., 2004).
Acanthoscelides obtectus			1			107	8	Introduced with contaminated seeds (Yus-Ramos et al., 2012). MRT from the literature (Yus-Ramos, 1977), sub *Acanthoscelides obsoletus*.
Achaearanea tepidariorum			1			93	5	Introduced as a Contaminant with potted plants (Nentwig, 2015), sub *Parasteatoda tepidariorum*. MRT from public databases (Serra, 2019), sub *Parasteatoda tepidariorum*.
Aedes (Stegomyia) albopictus				1		15	148	Introduced as a Stowaway with second-hand tyres and bamboos for horticulture (Ministerio para la Transición Ecológica, 2013; Skuhravá et al., 2010). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Alphitobius diaperinus			1			132	8	Minor pest of residues and common in chicken houses, feeds on waste and rotting organic material (Denux & Zagatti, 2010). Based on this we assign the Contaminant pathway. MRT from the literature (Cuní i Martorell, 1888).
Alphitobius laevigatus			1			66	2	Minor pest of residues and stored products (Denux & Zagatti, 2010). Based on this we assign the Contaminant pathway. MRT from public databases (Serra, 2019).

Amaurobius similis				1		46	3	Probably introduced with trade like other spiders, we don't know whether it is ecologically associated with specific commodities (soil, plants), we assign the Stowaway pathway. MRT from the literature (Barrientos, 1986).
Apate monachus			1			64	2	Phytophagous stem borer on trees (Denux & Zagatti, 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from public databases (Serra, 2019).
Aphis gossypii			1			33	3	Polyphagous pest of a wide range of crops (Coeur d'Acier et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the literature (Avinent et al., 1989).
Arocatus longiceps			1			11	1	Introduction possible linked to trade in the Barcelona harbour, although other pathways cannot be ruled out (Ribes & Pagola-Carte, 2008). MRT from the literature (Ribes & Pagola-Carte, 2008).
Belonochilus numenius					1	11	85	First reported in Europe in 2008, it has spread across the continent aided by the widespread presence of its host tree as an ornamental (Riba et al., 2015). MRT from the literature (Gessé et al., 2009).
Bipalium kewense			1			41	5	Probably introduced unintentionally with ornamental plants (Filella-Subirà, 1983). MRT from the literature (Filella-Subirà, 1983).
Bruchidius terrenus			1			8	4	Introduced with contaminates seeds (Yus-Ramos et al., 2012). MRT from the literature (Yus-Ramos et al., 2012).
Brunneria borealis				1		3	1	Possibly introduced on commodities or luggage (Fernández & Santaeufemina, 2016). MRT from the literature (Fernández & Santaeufemina, 2016).
Cacyreus marshalli			1			26	84	Probably introduced accidentally with host plants (Lopez-Vaamonde et al., 2010; Masó & Sarto, 1995). MRT from the literature (Masó & Sarto, 1995).
Caenoplana coerulea			1			8	5	Probably introduced unintentionally with soil and plants (Mateos et al., 2013). MRT from the literature (Mateos et al., 2013).
Cameraria ohridella			1	1		15	4	It is more likely an independent introduction rather than unaided spread from France (Olivella, 2004). Passive transport of this insect (in cars, trains, trucks) probably plays an important role in its expansions (Gilbert et al., 2004). Possibly also transported with contaminated plant material (Olivella, 2004; Šefrová & Laštůvka, 2001). MRT from the literature (Olivella, 2004).

Cartodere (Aridius) bifasciata			1			11	1	Detritivorous, found under bark (Denux & Zagatti, 2010). We assign the Contaminant pathway (possible introduction with plant material). MRT from the literature (Viñolas et al., 2008).
Ceratitis capitata			1			37	2	Introduced with contaminated fruits (Skuhravá et al., 2010). MRT from the literature (Carles-Tolrá, 1997).
Chalcionellus decemstriatus			1			34	3	Predator found on faeces and cadavers (Denux & Zagatti, 2010). We assign the Contaminant pathway (possibly introduced with spoiled food or similar). MRT from public databases (Serra, 2019).
Chilo suppressalis			1			37	9	Phytophagous pest of rice (Lopez-Vaamonde et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the literature (Pérez De-Gregorio et al., 1990).
Chlorophorus annularis			1			28	1	Probably introduced with contaminated plant material (Vives, 1995). MRT from the literature (Vives, 1995).
Corythucha ciliata					1	39	14	It spreads passively (wind-drift), accidental transport (clothes, cars…) is also reported (Rabitsch, 2008). We assign the Unaided pathway because we think it has played a bigger role in introducing the species. MRT from the literature (Ribes, 1980).
Cydalima perspectalis					1	5	31	Spread from France (Dinca et al., 2017). MRT from the literature (Dinca et al., 2017).
Dactylopius opuntiae			1			5	5	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Dactylotrypes longicollis			1			23	1	Introduced with contaminated seeds (Sauvard et al., 2010). MRT from public databases (Serra, 2019).
Drosophila hydei			1			40	2	Detritivorous (Skuhravá et al., 2010). We assign the Contaminant pathway (possible introduction with spoiled food or similar). MRT from the literature (M. Argemí et al., 2002).
Drosophila immigrans			1			40	1	Detritivorous on fruits (Skuhravá et al., 2010). We assign the Contaminant pathway (possible introduction with spoiled food or similar). MRT from the literature (M. Argemí et al., 2002).

Dryocosmus kuriphilus			1			7	6	Phytophagous species (Rasplus et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the literature (Pujade-Villar et al., 2013b).
Ephestia kuehniella			1			114	4	Detritivore, introduced with stored food (Lopez-Vaamonde et al., 2010). MRT from public databases (Serra, 2019), sub *Ephestia* (*Anagasta*) *kuehniella*.
Epichoristodes acerbella			1			44	5	Phytophagous species (Lopez-Vaamonde et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Eriosoma lanigerum			1			33	1	Pest of apple trees (Coeur d'Acier et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from public databases (Serra, 2019).
Euxesta pechumani			1			39	3	Detritivore on carrion and dung (Skuhravá et al., 2010). We assign the Contaminant pathway (possible introduction with spoiled food or similar). MRT from the literature (Carles-Tolrá, 1992).
Glycaspis brimblecombei					1	10	13	Spread from adjacent Spanish regions (Hurtado et al., 2010; Peris-Felipo et al., 2010). MRT from the literature (Peris-Felipo et al., 2010).
Gnathocerus cornutus			1			132	5	Detritivore in stored cereals (Denux & Zagatti, 2010). MRT from the literature (Cuní i Martorell, 1888).
Grapholita molesta			1			76	22	Phytophagous species (Lopez-Vaamonde et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Halyomorpha halys			1			3	18	Phytophagous species on fruit trees and ornamentals (Rabitsch, 2010b). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Harmonia axyridis					1	9	17	We found no records of its use for biological control in Catalonia. This species has considerable dispersal capacity (Ministerio para la Transición Ecológica, 2013; Roy & Migeon, 2010), Catalan populations are thought to have spread from France (Carbonell, 2013). MRT from the literature (Carbonell, 2013).

Hawaiia minuscula			1			6	8	Mainly introduced through the plant trade (Quiñonero et al., 2013; Quiñonero & López, 2015b). MRT from the literature (Quiñonero et al., 2013).
Helix (Helix) lucorum		1				9	2	Intentionally introduced for human consumption (Quiñonero & Ruiz, 2011). MRT from the literature (Quiñonero & Ruiz, 2011).
Helix (Helix) melanostoma			1			25	1	Pathway from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019). MRT from the literature (Neckheim, 1995).
Hermetia illucens			1			51	9	Probably spread with contaminated food (Leclercq, 1979; Navarro & Peris, 1991). MRT from the literature (Leclercq, 1979).
Hypoponera punctatissima			1			39	3	Introduction probably linked to the plant trade (Gómez & Espadaler, 2007). MRT from X. Espadaler (personal communication).
Ips typographus			1			30	2	Pest of trees (Riba, 1989). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from the literature (Riba, 1989).
Isodontia mexicana					1	33	3	Probably unaided spread from France (Gayubo & Izquierdo, 2006). MRT from (Carbonell, 2012).
Lasioderma serricorne			1			40	2	Introduced with stored food (Denux & Zagatti, 2010). MRT from public databases (Serra, 2019).
Lasius neglectus			1			29	24	Introduced with contaminated potted plants and soil (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Espadaler, 1999).
Leptinotarsa decemlineata					1	84	12	Likely spread from France (Grapputo et al., 2005). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Leptoglossus occidentalis			1			16	35	The main pathway of introduction is thought to be the maritime trade, possibly with multiple introductions and posterior translocations (Ministerio para la Transición Ecológica, 2013). Catalonian records probably represent an independent introduction rather than spread from adjacent regions (Lis et al., 2008), possibly originating from garden centres (Ribes & Escolà, 2005). MRT from the literature (Ribes & Escolà, 2005).
Linepithema humile			1			77	137	Introduced with trade of goods, soil, plants, etc (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Roura-Pascual et al., 2009).
Liriomyza trifolii			1			31	1	Polyphagous leaf miner (Skuhravá et al., 2010). We think it was probably introduced accidentally with their host plants as a Contaminant. MRT from public databases (Serra, 2019).

Lophocateres pusillus			1			85	3	Pest of stored products (Denux & Zagatti, 2010). MRT from public databases (Serra, 2019).
Lucasianus levaillanti			1			32	4	Likely introduced with imported trees (Vives, 1995). MRT from the literature (Vives, 1995).
Lyctus (Xylotrogus) brunneus			1			66	5	Introduced with contaminated wood (Español, 1956). MRT from the literature (Español, 1956).
Lyphia tetraphylla			1			70	4	Detritivore species (Denux & Zagatti, 2010). Possibly introduced with contaminated food. MRT from the literature (Español, 1949b).
Megabruchidius dorsalis			1			3	1	Probably introduced with contaminated plant material (Yus-Ramos & Carles-Tolrá, 2016). MRT from the literature (Yus-Ramos & Carles-Tolrá, 2016).
Megabruchidius tonkineus			1			3	1	Probably introduced with contaminated plant material (Yus-Ramos & Carles-Tolrá, 2016). MRT from the literature (Yus-Ramos & Carles-Tolrá, 2016).
Megachile sculpturalis				1	1	1	15	Its spread is probably a combination of unaided spread and transportation of contaminated timber (Aguado et al., 2018; Le Féon et al., 2018). MRT from the literature (Aguado et al., 2018; Ortiz-Sánchez et al., 2018).
Monomorium carbonarium			1			7	6	Possibly introduced with plant material (Miravete et al., 2013). MRT from the literature (Miravete et al., 2013).
Monomorium destructor				1		17	1	Introduced with trade (Espadaler, 2005; Ministerio para la Transición Ecológica, 2013). The ant was not associated with soil, potted plants or plant material (Espadaler, 2005), so we assign the Stowaway pathway. MRT from the literature (Espadaler, 2005).
Necrobia rufipes			1			70	5	Predator of insects that contaminate stored products (Denux & Zagatti, 2010). MRT from the literature (Español, 1949a).
Neophyllaphis podocarpi			1			8	3	Probably introduced with contaminated plant material (Pérez Hidalgo et al., 2015). MRT from the literature (Pérez Hidalgo et al., 2015).
Parectopa robiniella					1	18	4	Possibly spread from adjacent European countries (Olivella, 2003). MRT from the literature (Olivella, 2003).
Paromalus (Isolomalus) luderti			1			103	3	Detritivore species, found in decaying organic material (Denux & Zagatti, 2010). We think it was possibly introduced with contaminated commodities. MRT from T. Yélamos (personal communication).

Paysandisia archon			1			19	29	Accidental introduction, possibly with infested trees (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Guzmán, 2006).
Pentacora sphacelata				1		58	3	Introduced as a Stowaway (Rabitsch, 2008). MRT from the literature (Ribes, 1983).
Periplaneta americana				1		33	2	Probably introduced as a Stowaway (Rabitsch, 2010a). MRT from public databases (Serra, 2019).
Pheidole megacephala			1			124	1	Probably introduced unintetnionally with trade (Wetterer, 2012). We don't know whether it is ecologically associated with particular commodities (soil, plants), we assign the Stowaway pathway. MRT from the literature (Espadaler & Pradera, 2016).
Pheidole teneriffana				1		20	1	Present in disturbed areas (Rasplus et al., 2010). We don't know whether it is ecologically associated with particular commodities (soil, plants), we assign the Stowaway pathway. MRT from the literature (Espadaler & Collingwood, 2001).
Pholcus phalangioides				1		139	11	Probably introduced with trade like other spiders, we don't know whether it is ecologically associated with specific commodities (soil, plants), we assign the Stowaway pathway. MRT from public databases (Serra, 2019).
Phoracantha semipunctata			1			24	2	Probably introduced with infested trees (Vives, 1995). MRT from the literature (Vives, 1995).
Photinus inmigrans			1			1	8	Origin of the introduction uncertain, possibly introduced with plants or for research (Viñolas et al., 2018). All reported colonies have been found near fields of transgenic corn (Zaragoza-Caballero & Viñolas, 2018), so we think an introduction with contaminated plants may be more likely. MRT from the literature (Viñolas et al., 2018; Zaragoza-Caballero & Viñolas, 2018).
Phyllonorycter robiniella					1	18	4	Possibly spread from adjacent European countries (Olivella, 2003). MRT from the literature (Olivella, 2003).
Polygyra cereolus			1			7	3	Mainly introduced through the plant trade (Quiñonero & López, 2015a). MRT from the literature (Quiñonero & López, 2015a).
Pycnoscelus surinamensis			1			2	1	Probably introduced unintentionally with contaminated plant material (Pradera & Carcereny, 2018). MRT from the literature (Pradera & Carcereny, 2018).

Rhynchophorus ferrugineus			1			14	156	Introduction and further spread with contaminated plant trees (Ministerio para la Transición Ecológica, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Rhyzopertha dominica			1			70	1	Pest of stored products (Denux & Zagatti, 2010). MRT from the literature (Español, 1949a).
Rodolia cardinalis	1					70	6	Introduced for biological control (Español, 1949a; Roy & Migeon, 2010), sub *Rodolia* (*Macronovius*) *cardinalis*. MRT from the literature (Español, 1949a).
Saprinus (Saprinus) lugens			1			37	1	Detritivore on cadavers and faeces (Denux & Zagatti, 2010). We think it was possibly introduced with contaminated food. MRT from T. Yélamos (personal communication).
Sceliphron curvatum				1		14	12	Origin of the introduction uncertain (Castro, 2007), an introduction through accidental transport and posterior dispersal has been suggested (Carbonell, 2008). MRT from the literature (Castro, 2007).
Scyphophorus acupunctatus			1			12	8	Phytophagous species, probably introduced multiple times in Europe (Sauvard et al., 2010). MRT from the literature (Riba & Alonso, 2007).
Sipha flava			1			5	4	Pest of the sugar cane (Hernández-Castellano & Pérez, 2014). MRT from the literature (Hernández-Castellano & Pérez, 2014).
Sitophilus oryzae			1			70	1	Pest of stored grain (Sauvard et al., 2010). MRT from the literature (Español, 1949a).
Sitotroga cerealella			1			112	4	Pest of stored products (Carbonell, 2013; Lopez-Vaamonde et al., 2010). MRT from the literature (Carbonell, 2013).
Spermophora senoculata			1			27	2	Introduced as a Contaminant with potted plants (Nentwig, 2015). MRT from public databases (Serra, 2019).
Spodoptera littoralis					1	52	14	Probably spread from populations in the South of Spain (Sarto, 1984). MRT from public databases (Serra, 2019).
Steatoda grossa			1			100	4	Introduced as a Contaminant with fruits (Nentwig, 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Steatoda nobilis			1	1		24	5	Introduced as a Contaminant (with fruits and potted plants), and as a Stowaway in containers (Nentwig, 2015). MRT from the literature (Melic, 1995).
Stictocephala bisonia			1			33	3	Probably introduced with fruit tree cuttings (Mifsud et al., 2010). MRT from public databases (Serra, 2019), sub *Ceresa bubalus*.

Supella longipalpa				1		6	1	Probably introduced as a Stowaway (Rabitsch, 2010a). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Tapinoma melanocephalum			1			17	2	Introduction linked to trade (Ministerio para la Transición Ecológica, 2013), in some instances probably carried with plant material or products from the tropics (Espadaler & Espejo, 2002). MRT from the literature (Espadaler & Espejo, 2002).
Tenebroides mauritanicus			1			112	12	Pest of stored products (Denux & Zagatti, 2010). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Torymus sinensis					1	3	3	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Trachyopella (Trachyopella) straminea			1			37	6	Detritivore species (Skuhravá et al., 2010). Possibly introduced with rotting goods. MRT from the literature (Carles-Tolrá, 1994).
Tribolium (Stene) confusum			1			70	2	Pest of stored products (Denux & Zagatti, 2010). MRT from the literature (Español, 1949a).
Trichopoda pennipes			1			24	5	Origin of the introduction uncertain: spread from Italy or an independent introduction (Tschorsnig et al., 2000). A link with the horticulture trade has been suggested (Peris, 1998) and adopted in the present analysis. MRT from the literature (Peris, 1998).
Vespa velutina					1	7	115	Introduced in France with trade, with posterior spread along waterways (Ministerio para la Transición Ecológica, 2013). MRT from the literature (Pujade-Villar et al., 2013a).
Viteus vitifoliae					1	142	2	Spread from France (Mifsud et al., 2010; Piqueras, 2005). MRT from the literature (Carbonell, 2012).
Xylotrechus chinensis			1	1		7	1	Introduction linked to wood-packaging material and pallets, and the horticulture trade (Sarto & Torras, 2018). MRT from the literature (Sarto & Torras, 2018).
Zonitoides arboreus			1			19	5	Introduced through the horticulture trade (Quiñonero, López, & Ruiz, 2014). MRT from the literature (Quiñonero, López, & Ruiz, 2014).

(g) Terrestrial vertebrates: birds (N = 121 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Acridotheres ginginianus		1				13	2	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Estrada & Anton, 2007).
Acridotheres tristis		1				22	5	Mainly escaped from captivity (Santos et al., 2012). MRT from the literature (Herrando et al., 2011).
Agapornis fischeri		1				22	10	Escaped or irresponsibly dumped from captivity (Santos, 2008a). MRT from the literature (Clavell, 2002).
Agapornis personatus		1				17	1	Mainly escaped from captivity (Santos et al., 2012). MRT from the literature (Estrada et al., 2004).
Agapornis pullarius		1				17	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Sales, 2006).
Agapornis roseicollis		1				22	9	Escaped from captivity (Herrando et al., 2011). MRT from the literature (Herrando et al., 2011).
Aix galericulata		1			1	50	88	Catalan records would be a combination of escapes (Clavell, 2002; Estrada et al., 2004) and spread from other countries (Clavell, 2002; Herrando et al., 2011). The phenological pattern suggests that the majority of individuals are of wild origin (Herrando et al., 2011). MRT from the literature (Ferrer et al., 1986).
Aix sponsa		1				33	18	Mainly introduced from captivity (Herrando et al., 2011), also reported as ornamental (Grupo de Aves Exóticas, 2008). Some individuals may be native (Grupo de Aves Exóticas, 2008). MRT from the literature (Clavell, 2002).
Alectoris graeca	1					47	1	Released for hunting (Clavell, 2002; Cordero-Tapia, 1983). MRT from the literature (Cordero-Tapia, 1983).
Alopochen aegyptiaca		1				26	80	Multiple origins have been put forward for Catalan records: escapes, releases and other European populations (Estrada et al., 2004; Herrando et al., 2011). We think the most fitting pathway is Escape. MRT from the literature (Herrando et al., 2011).

Amandava amandava subsp. *amandava*		1				40	45	Escaped from captivity (R. Gutiérrez et al., 1995) sub *Amandava amandava*. It has been suggested that Catalan birds may derive from Spanish populations (Estrada et al., 2004), sub *Amandava amandava*). Without further information, we maintain an Escape pathway. MRT from the literature (Estrada et al., 2004) sub *Amandava amandava*.
Amazona aestiva		1				24	3	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Amazona amazonica		1				18	4	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Aymí & Herrando, 2005).
Amazona ochrocephala		1				18	1	Mainly escaped from captivity (Grupo de Aves Exóticas, 2008). MRT from the literature (Aymí & Herrando, 2005).
Anas bahamensis		1				24	4	Introduced from captivity (Estrada et al., 2004), probably from zoos (Herrando et al., 2011). MRT from the literature (Clavell, 2002).
Anas cyanoptera		1				25	4	Introduced from captivity (Anton, 2009; Clarabuch, 2011), escaped from zoos, urban parks or private collections (Herrando et al., 2011) Some individuals may be native (Grupo de Aves Exóticas, 2008). MRT from literature (Clavell, 2002).
Anas falcata		1				15	1	Possibly introduced from captivity (Gil-Velasco et al., 2015), although a natural origin cannot be ruled out (Gil-Velasco et al., 2015; Grupo de Aves Exóticas, 2007a). MRT from the literature (Sales, 2006).
Anas formosa		1				8	1	This species was usually regarded as an escape, though since the discovery of a migrant in 2005 caution is advised (de Juana & Comité de Rarezas de la Sociedad Española de Ornitología, 1987; Dies et al., 2007). Since the Catalan checklist (Gil-Velasco et al., 2015) considers it an introduction from captivity, we assign the Escape pathway. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

Anas rhynchotis		1				17	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Anas sibilatrix		1				23	3	Escaped from captivity (Aymí & Herrando, 2005). MRT from the literature (Aymí & Herrando, 2005).
Anser cygnoides		1				13	2	Introduced from captivity (Estrada & Anton, 2007). MRT from the literature (Estrada & Anton, 2007).
Anser indicus		1				10	6	Escaped from captivity (Clarabuch, 2011). MRT from the literature (Clarabuch, 2011).
Ara ararauna		1				17	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Aratinga acuticaudata		1				29	12	Escaped or irresponsibly dumped from captivity (Santos, 2006a). MRT from the literature (Estrada et al., 2004).
Aratinga aurea		1				24	1	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Aratinga erythrogenys		1				26	3	Escaped or irresponsibly dumped from captivity (Santos, 2006b). MRT from the literature (Estrada et al., 2004).
Aratinga holochlora		1				24	1	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Aratinga jandaya		1				11	1	Introduced from captivity (Anton, 2009). MRT from the literature (Grupo de Aves Exóticas, 2010).
Aratinga leucophthalmus		1				12	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Grupo de Aves Exóticas, 2008).
Aratinga mitrata		1				28	10	Escaped or irresponsibly dumped from captivity (Santos, 2006c). MRT from the literature (Clavell, 2002).
Aratinga nana		1				14	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Barnardius zonarius		1				12	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Grupo de Aves Exóticas, 2008).

Branta canadensis		1				22	37	Origin of the introduction uncertain, either an escape or spread from neighbouring countries (Herrando et al., 2011). We think the Escape pathway is more likely for this species. MRT from the literature (Copete, 2000).
Branta sandvicensis		1				12	1	Escaped from the zoo (Grupo de Aves Exóticas, 2008). MRT from the literature (Grupo de Aves Exóticas, 2008).
Cacatua galerita		1				18	5	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Aymí & Herrando, 2005).
Cairina moschata		1				25	42	Introduced in farms and as ornamental in public parcs and gardens (Estrada et al., 2004), the bulk of Catalan records belong to birds either escaped from captivity or released by their owners (Herrando et al., 2011). MRT from the literature (Estrada et al., 2004).
Callonetta leucophrys		1				15	2	Introduced from captivity (Clarabuch, 2011). MRT from the literature (Sales, 2006).
Carduelis yarrellii		1				24	1	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Chenonetta jubata		1				24	1	It is considered an Escape from captivity (Clavell, 2002). MRT from the literature (Clavell, 2002).
Chrysolophus amherstiae		1				15	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Sales, 2006).
Chrysolophus pictus		1				18	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Colinus virginianus	1					36	5	Released for hunting (Clavell, 2002). MRT from the literature (Clavell, 2002).
Columba livia		1				114	273	Introduced mainly from domestic stocks (Estrada et al., 2004). MRT from the literature (Ferrer, 2019).
Coturnix japonica	1					36	3	Released for hunting and hunting dog training (Clavell, 2002; Estrada et al., 2004). MRT from the literature (Clavell, 2002).
Cyanoliseus patagonus		1				25	10	Escaped or irresponsibly dumped from captivity (Santos, 2008b). MRT from the literature (Esteban, 1994).

Cyanopica cyanus		1				63	9	Probably escaped from captivity (Aymí & Herrando, 2003; Ferrer et al., 1986). MRT from the literature (Aymí & Herrando, 2003).
Cygnus atratus		1			1	31	22	Mainly escaped from captivity (Clavell, 2002; Estrada et al., 2004), although likely that part of the records belong to individuals coming from other introduced populations in Europe (Clavell, 2006). MRT from the literature (Clavell, 2002).
Dendrocygna autumnalis		1				19	1	Escape from captivity (Aymí & Herrando, 2003). MRT from the literature (Aymí & Herrando, 2003).
Dendrocygna bicolor		1				28	4	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Dendrocygna viduata		1				105	2	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Clavell, 2002).
Dromaius novaehollandiae subsp. *novaehollandiae*		1				18	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Emberiza bruniceps		1				57	3	Probably escaped from captivity (Ferrer et al., 1986). MRT from the literature (Ferrer et al., 1986).
Eophona migratoria		1				14	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Estrilda astrild		1				39	79	Escaped from captivity (Herrando et al., 2011). MRT from the literature (Ramos, 1998).
Estrilda caerulescens		1				25	1	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Estrilda melpoda		1				34	9	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Herrando et al., 2011).
Estrilda rhodopyga		1				17	3	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Estrilda troglodytes		1				25	14	Mainly escaped from captivity (Santos et al., 2012). MRT from the literature (Esteban, 1994).
Euplectes afer		1				25	34	Mainly escaped from captivity (Santos et al., 2012). MRT from the literature (Estrada et al., 2004).

Euplectes franciscanus		1				27	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Clavell, 2002).
Euplectes hordeaceus		1				20	1	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Martínez-Vilalta, 2002).
Euplectes jacksoni		1				21	1	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Clavell, 2002).
Euplectes macrourus		1				19	2	Introduced from captivity (Gil-Velasco et al., 2015), occasionally present in pet shops (Aymí & Herrando, 2003). MRT from the literature (Aymí & Herrando, 2003).
Euplectes nigroventris		1				14	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Sales, 2006).
Euplectes orix		1				24	5	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Gracula religiosa		1				19	1	Introduced from captivity (Anton, 2009). MRT from the literature (Clavell, 2002).
Lagonosticta senegala		1				13	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Estrada & Anton, 2007).
Lamprotornis chalybaeus		1				19	2	Mainly escaped from captivity (Santos et al., 2012). MRT from the literature (Aymí & Herrando, 2003).
Lamprotornis superbus		1				13	1	Escaped from captivity (Herrando et al., 2011). MRT from the literature (Herrando et al., 2011).
Leiothrix lutea		1				26	19	Escaped or irresponsibly dumped from captivity (Furquet, 2010). MRT from the literature (Clavell, 2002).
Leptoptilos crumeniferus		1				26	8	Origin uncertain (Clarabuch, 2011), frequently present in zoos, although natural dispersal cannot be ruled out (Aymí & Herrando, 2005; Martínez-Vilalta, 2002). MRT from the literature (Clavell, 2002).
Lonchura atricapilla		1				24	2	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Lonchura maja		1				25	2	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Clavell, 2002).

Lonchura malacca subsp. *malacca*		1				21	3	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Estrada et al., 2004), sub *Lonchura malacca*.
Lonchura nigriceps		1				21	1	Introduced from captivity (Estrada et al., 2004). MRT from (Clavell, 2002), sub *Lonchura bicolor nigriceps*.
Lonchura punctulata		1				28	1	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Martínez-Vilalta, 2001).
Meleagris gallopavo		1				8	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Melopsittacus undulatus		1				37	24	Escaped or irresponsibly dumped from captivity (Santos, 2009). MRT from the literature (Ramos, 1998).
Mycteria ibis		1				23	1	Escaped from captivity (Clavell, 2002). MRT from the literature (Clavell, 2002).
Myiopsitta monachus		1				44	208	Escaped or irresponsibly dumped from captivity (Santos, 2005). MRT from the literature (Santos, 2005).
Nandayus nenday		1				40	6	Escaped or irresponsibly dumped from captivity (Santos, 2006d). MRT from the literature (Ferrer, 2019).
Nymphicus hollandicus		1				21	13	Mainly escaped from captivity (Grupo de Aves Exóticas, 2008). MRT from the literature (Martínez-Vilalta, 2001).
Oena capensis		1				29	1	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Oxyura jamaicensis					1	36	30	Mainly spread from other European populations (Clavell, 2002; Herrando et al., 2011). Eradication measures against this species in the United Kingdom have caused a decrease of Catalan records (Herrando et al., 2011), indeed suggesting that the presence of this bird in Catalonia depends on migration from other populations rather than escapes or releases. MRT from the literature (Ferrer et al., 1986).
Padda oryzivora		1				60	2	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).

Parabuteo unicinctus subsp. *harrisi*		1				17	1	Used in falconry, with registered escapes (Santos et al., 2014). MRT from the literature (Sales, 2006).
Paroaria coronata		1				29	2	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Estrada et al., 2004).
Passer luteus		1				23	1	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Martínez-Vilalta, 2002).
Pavo cristatus		1				14	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Platycercus elegans		1				16	2	Introduced from captivity (Clarabuch, 2011). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Platycercus eximius		1				15	1	Introduced from captivity (Clarabuch, 2011). MRT from the literature (Sales, 2006).
Ploceus cucullatus		1				36	2	Mainly escaped from captivity (Santos et al., 2012). MRT from the literature (Aymí & Herrando, 2005).
Ploceus galbula		1				29	2	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Estrada et al., 2004).
Ploceus manyar		1				21	1	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Martínez-Vilalta, 2001).
Ploceus melanocephalus		1				14	3	Mainly escaped from captivity (Grupo de Aves Exóticas, 2008). MRT from the literature (Sales, 2006).
Ploceus vitellinus		1				24	1	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).
Poicephalus crassus		1				13	1	Escaped from an aviary (Grupo de Aves Exóticas, 2007b). MRT from the literature (Grupo de Aves Exóticas, 2007b).
Poicephalus senegalus subsp. *senegalus*		1				37	4	Escaped or irresponsibly dumped from captivity (Santos, 2008c), sub *Poicephalus senegalus*. MRT from the literature (Estrada et al., 2004).
Psephotus haematonotus		1				11	1	Introduced from captivity (Anton, 2009). MRT from the literature (Anton, 2009).

Psittacula alexandri		1				16	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Sales, 2006).
Psittacula krameri		1				43	80	Escaped or irresponsibly dumped from captivity (Santos, 2008d). MRT from the literature (Batllori & Nos, 1985).
Psittacus erithacus		1				22	4	Escaped from captivity (Martín, 2006). MRT from the literature (Clavell, 2002).
Pytilia melba		1				16	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Quelea erythrops		1				18	2	Introduced through the pet trade (Aymí & Herrando, 2005). MRT from the literature (Aymí & Herrando, 2005).
Quelea quelea		1				44	19	Escaped or irresponsibly dumped from captivity (Estrada et al., 2004). MRT from the literature (Estrada et al., 2004).
Rhea americana		1				15	1	Escaped from captivity (Grupo de Aves Exóticas, 2007a). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Sarkidiornis melanotos		1				16	1	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Grupo de Aves Exóticas, 2007a).
Serinus canaria		1				64	9	Escaped from captivity (Herrando et al., 2011). MRT from the literature (Ferrer, 2019).
Serinus dorsostriatus		1				19	1	Introduced from captivity (Estrada et al., 2004). MRT from the literature (Clavell, 2002).
Serinus mozambicus		1				36	6	Introduced through the pet trade (Estrada et al., 2004). MRT from the literature (Clavell, 2002).
Sicalis flaveola		1				20	1	Escaped from captivity (Martínez-Vilalta, 2002). MRT from the literature (Martínez-Vilalta, 2002).
Sporaeginthus subflavus		1				36	1	Probably escaped from captivity (Aymí & Herrando, 2003), sub *Amandava subflava*. MRT from the literature (Clavell, 2002), sub *Amandava subflava*.
Streptopelia roseogrisea		1				24	13	Widely kept as a pet or used in laboratories (Herrando et al., 2011). MRT from the literature (Clavell, 2002).

Streptopelia senegalensis		1				18	7	Possibly an escape from captivity, although natural dispersal from Africa cannot be ruled out (Aymí & Herrando, 2005). MRT from the literature (Aymí & Herrando, 2005).
Struthio camelus		1				15	1	Escaped from farms (Carbajo, 2009). MRT from the literature (Carbajo, 2009).
Tadorna radjah		1				24	1	Considered an escape from captivity (Clavell, 2002). MRT from the literature (Clavell, 2002).
Taeniopygia guttata		1				36	1	Introduced through the pet trade (Estrada et al., 2004). MRT from the literature (Estrada et al., 2004).
Threskiornis aethiopicus		1			1	49	32	Catalan records would be a combination of escapes from captivity and spread from adjacent countries (Estrada et al., 2004; Herrando et al., 2011). MRT from the literature (Estrada et al., 2004).
Trichoglossus haematodus		1				19	2	Introduced from captivity (Gil-Velasco et al., 2015). MRT from the literature (Aymí & Herrando, 2003).
Vidua chalybeata		1				19	2	Escaped from captivity (Grupo de Aves Exóticas, 2007b). MRT from the literature (Clavell, 2002).
Vidua macroura		1				24	3	Escaped from captivity (R. Gutiérrez et al., 1995). MRT from the literature (Clavell, 2002).

(h) Terresttrial vertebrates: mammals (N = 8 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Atelerix albiventris		1				12	3	Introduced as a pet (Ministerio para la Transición Ecológica, 2013). MRT from http://www.atelerix.org/es/mapa/ (Accessed 9 June 2019).
Hystrix cristata		1				5	1	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Marmota marmota					1	45	33	Introduced in the French Pyrenees, spread into Catalonia (Palomo et al., 2007). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Myocastor coypus		1			1	48	34	Introduced for fur farming, also spreading from France (Palazón et al., 2015; Palomo et al., 2007). MRT from the literature (Palazón et al., 2015).

Neovison vison		1				39	195	Introduced for fur farming (Ministerio para la Transición Ecológica, 2013; Palomo et al., 2007). MRT from the literature (Ministerio para la Transición Ecológica, 2013).
Procyon lotor		1				18	6	Introduced as a pet (Ministerio para la Transición Ecológica, 2013; Salgado, 2018). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Rattus norvegicus				1		114	125	Origin of the introduction uncertain, as a natural spread or as a stowaway on ships (Ministerio para la Transición Ecológica, 2013), we think the Stowaway pathway is more likely, since it is also present on islands (Palomo et al., 2007). MRT from the literature (Ferrer, 2019).
Tamias sibiricus		1				29	6	Introduced as a pet (Mori et al., 2018), sub Eutamias sibiricus. MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).

(i) Terrestrial vertebrates: reptiles (N = 28 species)

Species	Rel	Esc	Con	Sto	Un	MRT	RS	Details
Agrionemys horsfieldii		1				12	11	Introduced as a pet (Soler et al., 2010). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Apalone ferox		1				8	1	Introduced as a pet (M. Franch, 2016). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Caiman crocodilus		1				26	2	Pathway and MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Chelydra serpentina		1				20	13	Introduced as a pet (Martínez-Silvestre et al., 2015; Pleguezuelos et al., 2002). MRT from the literature (M. Franch, 2016).
Chrysemys picta		1				29	8	Introduced as a pet (M. Campos et al., 2013; Ministerio para la Transición Ecológica, 2013). MRT from the literature (M. Franch, 2016).
Cyclemys dentata		1				20	11	Introduced as a pet (Pleguezuelos et al., 2002). MRT from the literature (M. Franch, 2016).
Graptemys pseudogeographica		1				20	13	Introduced as a pet (M. Campos et al., 2013; Pleguezuelos et al., 2002). MRT from the literature (M. Franch, 2016).
Macrochelys temminckii		1				6	1	Introduced as a pet (M. Franch, 2016). MRT from the literature (M. Franch, 2016).
Mauremys reevesii		1				8	9	Introduced as a pet (M. Franch, 2016). MRT from the literature (M. Franch, 2016).

Pelodiscus sinensis		1				20	7	Introduced as a pet (Pleguezuelos et al., 2002). MRT from the literature (M. Franch, 2016).
Podarcis pityusensis		1				28	1	Origin of the introduction unknown (Carretero et al., 1991), though later reviews refer to it as an active introduction (Gosá et al., 2015; Pleguezuelos et al., 2002). We think an irresponsible dumping from terraria a likely pathway and thus assign the Escape pathway. MRT from the literature (Carretero et al., 1991).
Podarcis sicula			1			8	1	This species arrived inside olive trees imported from Italy (Carretero & Silva-Rocha, 2015; Rivera et al., 2011). MRT from the literature (Rivera et al., 2011).
Pseudemys concinna		1				11	4	Introduced as a pet (M. Campos et al., 2013). MRT from the literature (M. Franch, 2016).
Pseudemys floridana		1				35	5	Introduced as a pet (Pleguezuelos et al., 2002). MRT from the literature (M. Franch, 2016).
Pseudemys nelsonii		1				11	2	Introduced as a pet (M. Franch, 2016). MRT from the literature (M. Franch, 2016).
Terrapene carolina		1				22	22	Introduced as a pet (Soler et al., 2010). MRT from the literature (Martínez-Silvestre et al., 2001).
Testudo graeca subsp. ibera		1				30	4	Introduced as a pet (Soler et al., 2010). MRT from the literature (Martínez-Silvestre et al., 2001).
Testudo hermanni subsp. boettgeri		1				30	8	Introduced as a pet (Soler et al., 2010). MRT from the literature (Martínez-Silvestre et al., 2001).
Testudo marginata		1				23	1	Introduced as a pet (Soler et al., 2010). MRT from the literature (Martínez-Silvestre et al., 2001).
Trachemys decussata		1				10	2	Introduced as a pet (M. Campos et al., 2013; M. Franch, 2016). MRT from the literature (M. Franch, 2016).
Trachemys emolli		1				11	3	Introduced as a pet (M. Campos et al., 2013; M. Franch, 2016). MRT from the literature (M. Franch, 2016).
Trachemys scripta subsp. elegans		1				38	171	Introduced as a pet (M. Campos et al., 2013; Ministerio para la Transición Ecológica, 2013). MRT from the literature (M. Franch, 2016).
Trachemys scripta subsp. scripta		1				17	33	Introduced as a pet (M. Campos et al., 2013; Ministerio para la Transición Ecológica, 2013). MRT from the literature (M. Franch, 2016).
Trachemys scripta subsp. troosti		1				8	1	Introduced as a pet (M. Campos et al., 2013; Ministerio para la Transición Ecológica, 2013). MRT from the literature (M. Franch, 2016).

Varanus juxtindicus		1				8	1	Introduced as a pet (Soler & Martínez-Silvestre, 2013). MRT from the literature (Soler & Martínez-Silvestre, 2013).
Varanus niloticus		1				25	2	Introduced as a pet (Soler & Martínez-Silvestre, 2013). MRT from the EXOCAT database (http://exocatdb.creaf.cat/base_dades/ Accessed June 2019).
Varanus salvator		1				11	2	Introduced as a pet (Soler & Martínez-Silvestre, 2013). MRT from the literature (Soler & Martínez-Silvestre, 2013).
Varanus Varanus exanthematicus		1				19	11	Introduced as a pet (Soler & Martínez-Silvestre, 2013). MRT from (Martínez-Silvestre et al., 2003).

Table S1.2. Variance Inflation Factor (VIF) for the Redundancy analysis (RDA) including total alien species richness (total number of alien species in each 10-km UTM cell, with all pathways pooled together) as an explanatory variable (not shown in the main text). The removal of explanatory variables followed the procedure described in the main text (removal of variables till we achieved Variance Inflation Factor < 10): a satisfactory VIF was reached after removing mean temperature and the UTM Y coordinate. This RDA is globally significant, with 3 significant canonical axes (all significant axes, $p < 0.05$), and has $R^2_{adj} = 0.826$. TOTAL indicates total species richness, the rest of explanatory variables follow the abbreviations in Table 2.1.

Variable	VIF
RAINFALL	6.385
ALTITUDE	7.574
DISTCOAST	4.401
DISTROAD	1.575
DISTWATER	1.399
POPDENS	2.281
CROPCOVER	2.625
URBANCOVER	3.163
UTMX	2.469
TOTAL	3.838

Table S1.3. Partitioning of correlations, and importance of the ordination axes, for the Redundancy analysis (RDA) including the total number of alien species per grid cell (not shown in the main text).

Partitioning of correlations:									
	Inertia	Proportion							
Total	5.000	1.000							
Constrained	4.156	0.831							
Unconstrained	0.844	0.169							
Eigenvalues, and their contribution to the correlations									
Importance of components:									
	RDA1	RDA2	RDA3	RDA4	RDA5	PC1	PC2	PC3	PC4
Eigenvalue	3.681	0.316	0.138	0.011	0.010	0.405	0.248	0.141	0.050
Proportion Explained	0.736	0.063	0.028	0.002	0.002	0.081	0.050	0.028	0.010
Cumulative Proportion	0.736	0.799	0.827	0.829	0.831	0.912	0.962	0.990	1.000
Accumulated constrained eigenvalues									
Importance of components:									
	RDA1	RDA2	RDA3	RDA4	RDA5				
Eigenvalue	3.681	0.316	0.138	0.011	0.010				
Proportion Explained	0.886	0.076	0.033	0.003	0.002				
Cumulative Proportion	0.886	0.962	0.995	0.998	1.000				

Table S1.4. Pairwise differences in range size among groupings through post-hoc Tukey contrasts of slopes (rate of increase in range size over time): slopes followed by the same letter did not differ significantly (Tukey contrast: p-v > 0.05). Slopes were calculated at the scale of the response (undoing the ln-transformation), and are presented with ± 1 standard error. Together with pairwise differences in slopes, we also the approximate the effect size of the association between groups and pathways through Cramér's V (see main text for the full details).

(a) Unpooled taxonomic groups (ANCOVA: R^2_{adj} = 0.376; association of medium strength between pathways and unpooled taxonomic groups, effect size: Cramér's V = 0.389).

Group	Slope	
Aquatic invertebrates	0.23 ± 0.091	ab
Amphibians	0.107 ± 0.069	ab
Aquatic fish	0.179 ± 0.037	b
Aquatic plants	0.135 ± 0.036	b
Birds	0.115 ± 0.022	b
Mammals	0.299 ± 0.141	ab
Reptiles	0.354 ± 0.253	ab
Terrestrial invertebrates	-0.002 ± 0.017	ab
Terrestrial plants	0.078 ± 0.005	b

(b) Animals and plants (N = 322 and 547 species, respectively; ANCOVA: R^2_{adj} = 0.319; association of weak strength between pathway and group (animal and plant); effect size: Cramér's V = 0.184).

Group	Slope	
Animal	0.22 ± 0.063	a
Plant	0.271 ± 0.03	a

(c) Aquatic and terrestrial (N = 83 and 786 species, respectively; ANCOVA: R^2_{adj} =0.339; association of medium strength between pathway and habitat (terrestrial vs. aquatic); effect size: Cramér's V = 0.358).

Group	Slope	
Aquatic	0.754 ± 0.267	a
Terrestrial	0.237 ± 0.025	a

(d) Invertebrates and vertebrates (N = 200 and 122 species, respectively, analysis restricted to animals; ANCOVA: R^2_{adj} = 0.272; association of high strength between pathway and animal groups (vertebrate vs. invertebrate); effect size: Cramér's V = 0.890).

Group	Slope	
Invertebrate	0.007 ± 0.019	a
Vertebrate	1.433 ± 0.467	b

Table S1.5. Variance Inflation Factor (VIF) for the Redundancy analysis (RDA) shown in the main text. Explanatory variables follow the abbreviations in Table 2.1.

Variable	VIF
RAINFALL	5.843
ALTITUDE	6.762
DISTCOAST	4.026
DISTROAD	1.574
DISTWATER	1.3
POPDENS	2.248
CROPCOVER	2.578
URBANCOVER	2.855
UTMX	2.429

Table S1.6. Partitioning of correlations, and importance of the ordination axes, for the Redundancy analysis (RDA) shown in the main text.

Partitioning of correlations:

	Inertia	Proportion
Total	5.000	1.000
Constrained	3.029	0.606
Unconstrained	1.971	0.394

Eigenvalues, and their contribution to the correlations

Importance of components:

	RDA1	RDA2	RDA3	RDA4	RDA5	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.620	0.309	0.081	0.011	0.008	1.256	0.351	0.219	0.097	0.049
Proportion Explained	0.524	0.062	0.016	0.002	0.002	0.251	0.070	0.044	0.019	0.010
Cumulative Proportion	0.524	0.586	0.602	0.604	0.606	0.857	0.927	0.971	0.990	1.000

Accumulated constrained eigenvalues

Importance of components:

	RDA1	RDA2	RDA3	RDA4	RDA5
Eigenvalue	2.620	0.309	0.081	0.011	0.008
Proportion Explained	0.865	0.102	0.027	0.004	0.003
Cumulative Proportion	0.865	0.967	0.994	0.997	1.000

Supplementary figures

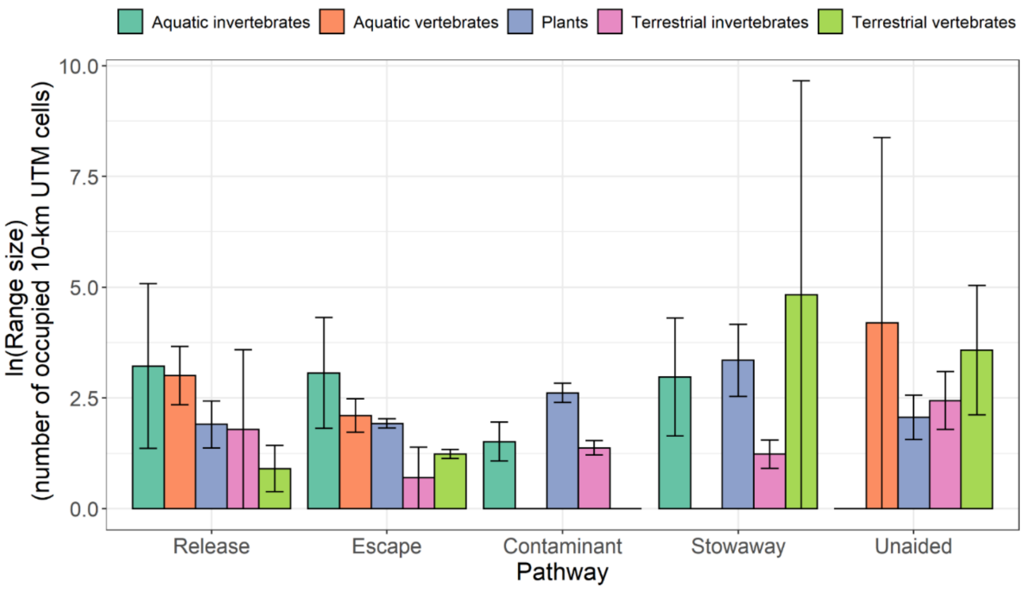


Fig. S1.1. Interaction graph for pathway x group, showing mean range size ± 1 standard error of the mean (range size was ln-transformed prior to the calculation of means and standard errors). Note out of a total of 25 estimations of mean range size, 10 estimations were based on a sample size lower than 10 species, and that there was no data for 3 pathway x group combinations (see Table 2.2 in the main text).

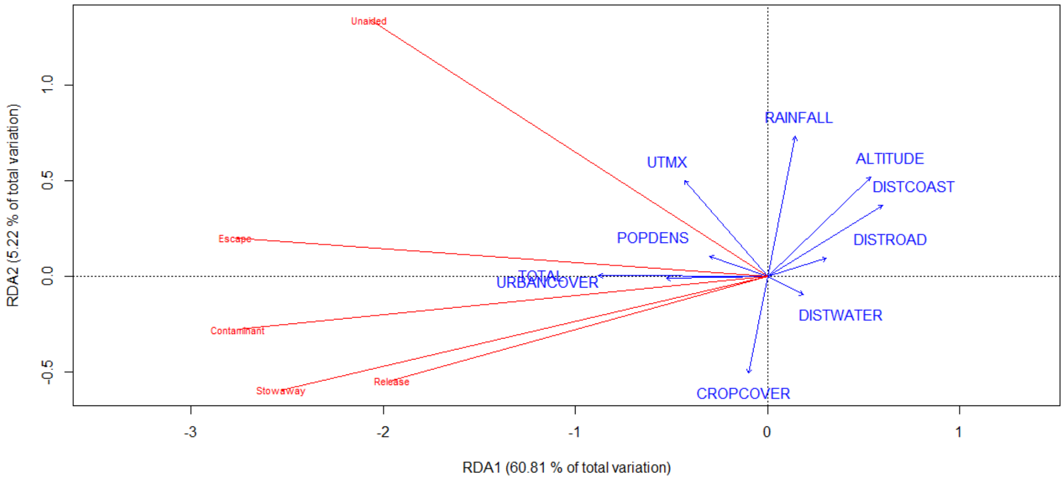


Fig. S1.2. RDA correlation biplot including the total number of alien species per grid cell (not shown in the main text), featuring the first two canonical axes (66% of total variation). Explanatory variables follow the abbreviations in Table 2.1. This analysis is restricted to 10-km UTM cells with more than 40% of their surface on Catalan land (N = 327 cells).

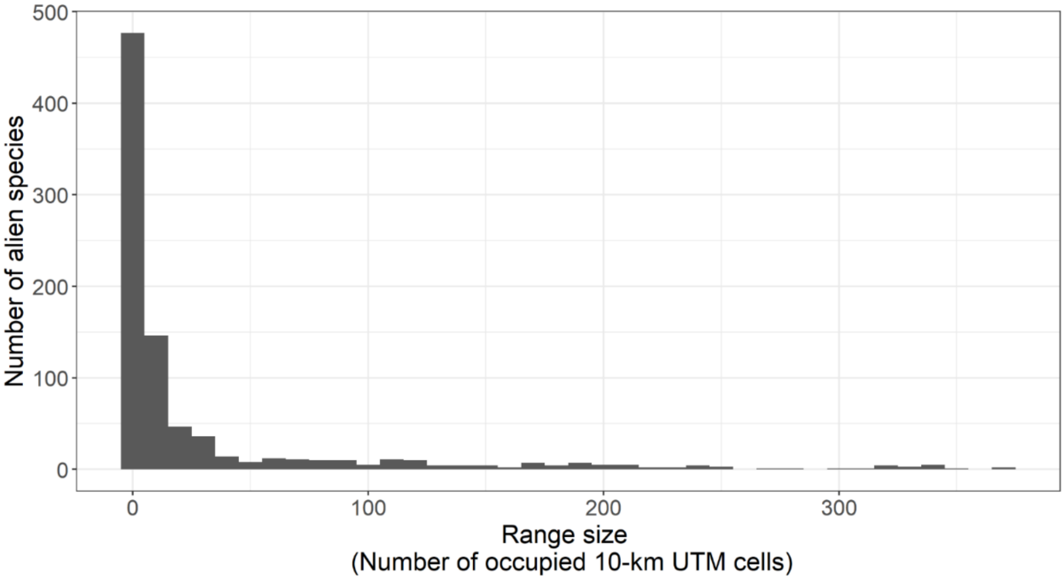


Fig. S1.3. Histogram of range sizes for the 869 alien species included in our dataset. The majority of species have small ranges, for instance, 95% of species are present in less than half of the total number of 10-km UTM cells in our study area (total number of 10-km UTM cells = 381). Only around 2% of species are present in over 80% of our study area.

Supplementary discussion

The supplementary ANCOVA models relating range size to the original taxonomic groups and the alternative groupings (animals vs. plants, terrestrial vs. aquatic aliens, vertebrates vs. invertebrates) yielded additional insights (Table S1.4)

The contribution of pathways was similar between aquatic and terrestrial environments, except for the release (25% in aquatic vs 2% in terrestrial) and escape (37% in aquatic vs 65% in terrestrial) pathways.

Within animals, vertebrates reached higher ranges than invertebrates, although in this case association with pathways might not be a suitable explanation, and research is lacking to provide robust suggestions. One possibility is differences in traits between taxonomic groups, such as dispersal capacity. Similar range size in animals and plants may be due to the weak association between pathways and the binary taxonomic grouping (animal vs. plant; Table S1.4b). Aquatic alien species reached higher ranges than terrestrial aliens, possibly due to extensive targeting of aquatic ecosystems for deliberate introductions (Clavero & García-Berthou, 2006; García-Berthou et al., 2005). Moreover, the proportion of escaped species in aquatic aliens was around half that of terrestrial aliens.

Appendix 2

Supplementary Material for Chapter 3

This Appendix contains

Supplementary Methods

Tables S2.1-S2.8

Figures S2.1-S2.4

Supplementary Discussion

Supplementary methods

Calculation of historical landscape variables

Historical landscape change was quantified as the percentage of area with progressive, regressive or no changes (within radii of 50 m around sampling points). This was assessed by combining reclassified versions of the original land-cover maps. Thus, maps were reclassified into five human disturbance classes (Pino et al., 2009): (1) very low, i.e., natural habitats; (2) low, including secondary natural habitats (cleared forests and scrublands) and deforestations; (3) medium, corresponding to recently burned forests and mowed agricultural lands with secondary grassland communities; (4) high, corresponding to croplands and plantations (of either *Populus* spp. or *Platanus* spp.), non-vegetated beaches and bare soil areas; and (5) very high, including built-up and leisure areas, and transport infrastructures. These reclassified maps were combined in a single human disturbance change map, in which changes were classified as either progressive, regressive, or no change when they corresponded to, respectively, an increase, a decrease or no variations in the human disturbance values.

Calculation of pairwise trait covariation

We assessed independence between categorical traits by gathering counts across all categories in two-way contingency tables, and calculating significance (through Chi-squared tests) and effect size of the association (through Cramér's V). We also assessed whether plants were over-represented in any combination of categories through mosaic plots and standardized Pearson residuals (Friendly & Meyer, 2016). Mosaic displays show the frequencies in contingencies tables through a set of rectangular tiles, whose area is proportional to the cell frequency (i.e. the higher the counts for a given combination of categories, the greater the area). We identified combinations of categories that where over- and/or underrepresented, by colouring tiles that had significantly high standardized Pearson residuals ($|r| > 2$): blue (positive residuals) or red (negative residuals). The residuals came from Chi-Square tests of independence. Blue indicated overrepresentation while red indicated underrepresentation (i.e. significantly more or less counts than expected, respectively, compared to a model of statistical independence).

We assessed correlation between continuous variables through Pearson's correlation.

We assessed whether continuous variables differ in their mean value across levels of the categorical variables, through one-way ANOVA, Tukey pairwise contrasts, and eta-squared (η^2, as a measure of effect size of the ANOVA).

We calculated Cramér's V and eta-squared with the 'DescTools' package (Signorell & mult. al., 2022), and Tukey pairwise contrasts with the 'emmeans' package (Lenth, 2023). We assessed patterns of overrepresentation between categorical variables with the 'vcd' package (D. Meyer et al., 2020). We plotted covariation between introduction pathways and minimum residence time and plant traits with the 'ggpubr' package (Kassambara, 2023).

Methodological details on the acquisition and processing of species occurrence and climatic data.

We followed the relevant sections of published guidelines (Feng et al., 2019).

(A) Occurrence data

A1) Source of occurrence data

Global Biodiversity Information Facility (GBIF, 2023), with the ‘rgbif’ package (Chamberlain et al., 2023).

A2) Download date; version of data source

24 August 2023

A3) Basis of records

We removed fossil occurrences, plants in cultivation, and absences, with the ‘tidyverse’ package (Wickham et al., 2019).

A4) Spatial extent

Global, excluding mainland Spain. Polygons delimiting the native ranges were taken from the Taxonomic Database Working Group (Brummitt, 2001).

A5) Temporal range

We did not filter occurrences based on year.

A6-1) Duplicate coordinates.

We removed duplicate coordinates with the package ‘tidyverse’ (Wickham et al., 2019).

A6-2) Spatial and environmental outliers, error

We did not address the spatial distribution of points, which would be unfeasible given the large sample size, and the lack of independent fine-scale distribution data for comparison. We think that we prevented some errors by excluding from our initial download some large citizen-science datasets (iNaturalist, Pl@ntnet). Such datasets may be prone to including mistaken identifications, and cultivated plants in private or public gardens.

A6-3) Spatial coordinates and uncertainty

We excluded occurrences without coordinates or with geospatial issues from our GBiF download (GBIF, 2023), using the ‘rgbif’ package (Chamberlain et al., 2023). After the download, we used the ‘CoordianteCleaner’ package (Zizka et al., 2019) to remove coordinates located in country centroids and biodiversity institutions (2-km buffer), or located in the open sea (buffland polygons). Regarding coordinate uncertainty, we kept coordinates without data on uncertainty, and when such data was provided, we excluded coordinates with more uncertainty than the resolution of the bioclimatic raster, using the ‘tidyverse’ package (Wickham et al., 2019). Raster resolution changes with latitude, so we calculated the threshold of unacceptable uncertainty (in meters) with the following formula (taken from: https://opendem.info/arc2meters.html): cosinus(LAT * PI / 180) * 1852 * RES; where LAT is the latitude, PI is a constant to convert latitude into radians ($\pi = 3.141593$), and RES is the resolution of the raster in arc-minutes (2.5 in our case).

A7-1) Sampling bias

We did not address sampling bias.

A7-2) Spatial autocorrelation

We did not address the spatial distribution of the points (see sections A61-A63 for filtering procedures). We did not address the spatial autocorrelation in bioclimatic variables extracted on those points either (Sillero & Barbosa, 2021).

(B) Environmental data

B1) Source

WorldClim version 2.1 (Fick & Hijmans, 2017)

B2) Download date; version of data source

Downloaded with the ‘geodata’ package (Hijmans et al., 2023), on 28th August 2023.

B3) Spatial resolution

2.5 arc-minutes (around 4.5 km at the Equator).

B4) Temporal range

1970-2000

Supplementary tables

Table S2.1. Effect of buffer size on land-cover values of urban and cropland (2009 values), tested with a likelihood ratio test that compared a binomial GLM with buffer a categorical factor (50-m, 500-m, 1000-m) vs. an intercept-only binomial GLM.

Land-cover	Likelihood ratio test p-value
Urban (2009)	0.834
Cropland (2009)	0.778

Table S2.2. Contingency table for the analysis of temporal trends (Fig. 3.2 in the main text). Abbreviations: AgriForest = Agriculture or Forestry.

Introduction period	Pathway	N
Before 1500	AgriForest	55
Before 1500	Gardening	18
Before 1500	Unintentional	34
1501-1900	AgriForest	36
1501-1900	Gardening	54
1501-1900	Unintentional	31
1901-1984	AgriForest	38
1901-1984	Gardening	142
1901-1984	Unintentional	110
1985-2019	AgriForest	32
1985-2019	Gardening	397
1985-2019	Unintentional	99

Table S2.3. Correlation matrix among environmental variables describing the invaded niche in the Barcelona province (N = 190 invaded plots). Land-cover variables were calculated across three buffer sizes (50m, 500m, 1000m).

	Elevation	Cropland 1956.50m	Urban 1956.50m	Cropland 1993.50m	Urban 1993.50m	Cropland 2009.50m	Urban 2009.50m	Cropland 1956.500m	Urban 1956.500m	cropland. 993.500m	Urban 1993.500m	Cropland 2009.500m	Urban 2009.500m	Cropland 1956.1000m	Urban 1956.1000m	cropland. 993.1000m	Urban 1993.1000m	Cropland 2009.1000m	Urban 2009.1000m	Progressive 1956.2009.50m	Regressive 1956.2009.50m	No changes 1956.2009.50m	Progressive 1993.2009.50m	Regressive 1993.2009.50m	No changes 1993.2009.50m	Distance stream	Distance road	Longitude	Latitude	Annual temperature	Annual rainfall	Annual radiation
Elevation	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 1956.50m	.01	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 1956.50m	-.11	-.28	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 1993.50m	.14	.66	-.23	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 1993.50m	-.20	-.11	.63	-.46	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 2009.50m	.17	.59	-.23	.78	-.39	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 2009.50m	-.27	-.02	.60	-.35	.83	-.43	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 1956.500m	-.12	.62	-.21	.48	-.14	.38	-.04	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 1956.500m	-.25	-.22	.78	-.29	.61	-.28	.57	-.30	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 1993.500m	.10	.47	-.21	.63	-.35	.54	-.30	.80	-.35	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 1993.500m	-.42	-.11	.56	-.38	.71	-.39	.68	-.17	.79	-.50	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 2009.500m	.19	.41	-.18	.57	-.34	.66	-.33	.67	-.32	.90	-.52	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 2009.500m	-.49	-.01	.48	-.32	.64	-.40	.74	-.001	.68	-.37	.91	-.48	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 1956.1000m	-.25	.48	-.11	.37	-.07	.29	.01	.92	-.21	.73	-.07	.60	.10	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 1956.1000m	-.29	-.19	.71	-.26	.55	-.24	.51	-.26	.95	-.32	.75	-.30	.65	-.21	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 1993.1000m	.02	.37	-.14	.49	-.23	.42	-.21	.74	-.31	.91	-.39	.82	-.28	.80	-.31	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 1993.1000m	-.51	-.08	.51	-.31	.58	-.32	.61	-.11	.77	-.43	.93	-.46	.87	-.02	.80	-.40	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cropland 2009.1000m	.14	.34	-.12	.44	-.23	.52	-.24	.64	-.29	.84	-.42	.90	-.38	.67	-.30	.92	-.45	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urban 2009.1000m	-.59	.003	.43	-.24	.53	-.32	.63	.06	.67	-.29	.85	-.40	.92	.16	.70	-.26	.94	-.38	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Progressive 1956.2009.50m	.04	.25	-.20	.12	-.30	-.08	-.37	.20	-.19	.17	-.18	.02	-.17	.15	-.19	.13	-.17	.02	-.14	1	.	.	.	.	.	.	.	.	.	.	.	.
Regressive 1956.2009 50m	-.14	.06	-.08	-.32	.47	-.37	.65	.02	.03	-.27	.33	-.32	.44	.03	.02	-.21	.29	-.26	.37	-.33	1	.	.	.	.	.	.	.	.	.	.	.

No changes 1956.2009 50m	.19	-.11	.25	.26	-.18	.48	-.30	-.18	.10	.09	-.20	.27	-.32	-.20	.10	.02	-.18	.19	-.29	-.36	-.65	1	.	.	.	.	.	.	.	.	.	.
Progressive 1993.2009 50m	.03	.006	-.17	.21	-.19	-.10	-.31	.13	-.14	.18	-.14	-.01	-.10	.13	-.14	.13	-.13	-.05	-.06	.55	-.17	-.30	1	.	.	.	.	.	.	.	.	.
Regressive 1993.2009 50m	-.07	.08	-.05	-.04	-.16	-.13	.28	.14	-.09	.02	-.02	-.03	.15	.14	-.08	.02	.04	-.01	.14	-.05	.47	-.39	-.18	1	.	.	.	.	.	.	.	.
No changes 1993.2009 50m	.06	-.01	.17	-.10	.27	.21	.04	-.19	.18	-.15	.12	.05	-.04	-.20	.16	-.12	.05	.06	-.08	-.37	-.23	.54	-.65	-.59	1	.	.	.	.	.	.	.
Distance stream	-.26	-.11	.14	-.14	.09	-.15	.16	-.11	.10	-.12	.14	-.15	.17	.03	.10	.006	.18	-.07	.22	-.06	.04	-.03	-.10	.09	.003	1	.	.	.	.	.	.
Distance road	.05	-.22	-.06	-.13	-.11	-.05	-.14	-.37	.0003	-.26	-.07	-.18	-.13	-.34	.07	-.22	-.02	-.17	-.09	-.14	-.09	.17	-.10	-.08	.15	.37	1	.	.	.	.	.
Longitude	-.17	-.23	.07	-.23	.17	-.34	.17	-.25	.09	-.29	.20	-.39	.19	-.22	.08	-.23	.16	-.34	.17	-.09	.11	-.14	-.009	.006	-.002	.07	.14	1	.	.	.	.
Latitude	.79	-.14	-.007	.03	-.07	.02	-.18	-.19	-.14	.006	-.26	.05	-.33	-.24	-.19	.003	-.37	.05	-.43	-.02	-.11	.13	.06	-.09	.03	-.26	.04	.20	1	.	.	.
Anual temperature	-.95	.07	.11	-.09	.19	-.12	.28	.17	.26	-.06	.42	-.16	.49	.28	.31	-.01	.52	-.12	.60	-.01	.14	-.18	-.05	.10	-.04	.28	-.03	.09	-.87	1	.	.
Anual rainfall	.58	-.14	-.14	-.04	-.11	-.09	-.13	-.28	-.23	-.12	-.27	-.11	-.32	-.37	-.26	-.15	-.36	-.13	-.41	-.07	.003	.06	-.02	-.02	.03	-.17	.17	.55	.67	-.68	1	.
Anual radiation	.45	.15	-.17	.16	-.22	.27	-.25	.08	-.27	.18	-.37	.30	-.39	-.01	-.27	.11	-.40	.25	-.45	.12	-.13	.13	.02	-.03	.01	-.16	-.14	-.81	.03	-.39	-.23	1

Table S2.4. Effect of the inclusion of a quadratic term to a single-variable model containing a standardized linear term, in terms of R^2, Akaike Information Criterion corrected for small sample sizes (AICc), and whether the 95% confidence interval for the quadratic terms overlapped with zero. This was done for **a)** binomial GLMs relating the proportion of gardening non-native plants to environmental variables (pathway-specific differences in the invaded niche), and **b)** PGLS models relating invasion success (measured in three complementary ways) to introduction pathways and other non-native plant attributes.

(a)

Variable	pseudo-R^2 (linear term)	pseudo-R^2 (linear + quadratic term)	AICc difference (quadratic - linear)	95% Confidence interval
% Urban (2009)	0.004	0.008	0.152	overlaps 0
% Cropland (2009)	0.023	0.027	0.318	overlaps 0
Longitude	0.001	0.001	1.917	overlaps 0
Elevation	0.002	0.003	1.659	overlaps 0
Distance to nearest main stream	0.017	0.032	-3.857	does not overlap 0
Distance to nearest main road	0.014	0.014	2.034	overlaps 0
% Regressive changes (1956-2009)	0.005	0.021	-4.615	does not overlap 0
% No changes (1956-2009)	0.002	0.012	-1.778	does not overlap 0

(b)

Model	Variable	R^2_{adj} (linear term)	R^2_{adj} (linear + quadratic term)	AICc difference (quadratic - linear)	95% Confidence interval
Area of occupancy (10-km, log-transformed)	Minimum residence time (MRT)	0.117	0.112	1.686	overlaps 0
Area of occupancy (10-km, log-transformed)	Height	0.011	-0.001	2.232	overlaps 0
Area of occupancy (10-km, log-transformed)	Native niche breadth	0.086	0.075	2.230	overlaps 0
Habitat range (log-transformed)	Minimum residence time (MRT)	0.094	0.086	2.020	overlaps 0
Habitat range (log-transformed)	Height	0.006	-0.007	2.261	overlaps 0
Habitat range (log-transformed)	Native niche breadth	0.051	0.038	2.273	overlaps 0
Invaded climatic niche breadth (log-transformed)	Minimum residence time (MRT)	0.103	0.093	2.121	overlaps 0
Invaded climatic niche breadth (log-transformed)	Height	0.004	-0.003	1.849	overlaps 0
Invaded climatic niche breadth (log-transformed)	Native niche breadth	0.025	0.017	1.924	overlaps 0

Table S2.5. Model selection tables. Given the large amount of fitted models (> 200 for invasion success, and > 1600 for the invaded niche), only the models used for the multimodel inference procedure are presented (i.e. those with delta ≤ 6). Note that weights were not renormalized to this "best subset". Abbreviations: AICc = Akaike Information Criterion corrected for small sample sizes, df = Degrees of freedom, logLik = maximum value of the log-likelihood function, LRT = likelihood ratio test

(a) Invaded niche

Model	df	logLik	AICc	Delta	Weight	McFadden pseudo-R^2	LRT
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat	6	-178.544	369.547	0.742	0.041	0.12	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	8	-177.013	370.821	2.016	0.022	0.128	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	10	-174.808	370.845	2.04	0.022	0.138	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	12	-172.577	370.918	2.113	0.021	0.149	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat	7	-178.207	371.03	2.225	0.02	0.122	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Elevation x Habitat	8	-177.216	371.228	2.423	0.018	0.127	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude	7	-178.323	371.261	2.456	0.018	0.121	0
% Cropland (2009) + Distance to nearest stream + Distance to	9	-176.162	371.325	2.52	0.017	0.132	0

nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2							
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009)	7	-178.441	371.497	2.692	0.016	0.121	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2	7	-178.482	371.58	2.776	0.015	0.12	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat	7	-178.516	371.647	2.842	0.014	0.12	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	10	-175.51	372.249	3.445	0.011	0.135	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	9	-176.702	372.404	3.599	0.01	0.129	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	9	-176.78	372.56	3.756	0.009	0.129	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	11	-174.543	372.569	3.765	0.009	0.14	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Elevation x Habitat	9	-176.8	372.599	3.795	0.009	0.129	0

% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009)	8	-177.906	372.608	3.803	0.009	0.123	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	11	-174.564	372.611	3.807	0.009	0.14	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	13	-172.357	372.782	3.978	0.008	0.151	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009)	11	-174.665	372.813	4.009	0.008	0.139	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	11	-174.683	372.849	4.045	0.008	0.139	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009) + Elevation x Habitat	13	-172.42	372.908	4.103	0.008	0.15	0
% Cropland (2009) + Distance to nearest stream + Distance to	8	-178.064	372.924	4.119	0.008	0.122	0

nearest stream ^ 2 + Elevation + Habitat + Longitude							
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	11	-174.729	372.942	4.137	0.008	0.139	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2	8	-178.079	372.954	4.15	0.008	0.122	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	13	-172.447	372.961	4.157	0.007	0.15	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + Elevation x Habitat	9	-176.99	372.979	4.175	0.007	0.128	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	9	-177.001	373.001	4.197	0.007	0.128	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009)	9	-177.009	373.017	4.213	0.007	0.128	0
% Cropland (2009) + Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat	8	-178.143	373.081	4.276	0.007	0.122	0
% Cropland (2009) + Distance to nearest stream + Distance to	8	-178.158	373.112	4.308	0.007	0.122	0

nearest stream ^ 2 + Elevation + Habitat + Elevation x % Cropland (2009)						
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	10	-175.976	373.181	4.376	0.007	0.133	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	13	-172.562	373.192	4.388	0.007	0.15	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Urban (2009)	8	-178.226	373.247	4.443	0.006	0.122	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009) + Elevation x Habitat	9	-177.127	373.255	4.45	0.006	0.127	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2	8	-178.233	373.262	4.458	0.006	0.122	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + Elevation x Habitat	9	-177.142	373.284	4.479	0.006	0.127	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	10	-176.051	373.332	4.527	0.006	0.132	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 +	9	-177.213	373.426	4.621	0.006	0.127	0

Elevation + Habitat + Elevation x Habitat							
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude	8	-178.32	373.436	4.632	0.006	0.121	0
% Cropland (2009) + Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	10	-176.115	373.46	4.655	0.006	0.132	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009) + Elevation x % Urban (2009)	8	-178.343	373.482	4.677	0.006	0.121	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009)	10	-176.127	373.482	4.678	0.006	0.132	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x % Cropland (2009)	10	-176.156	373.542	4.737	0.006	0.132	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Urban (2009)	8	-178.387	373.57	4.765	0.006	0.121	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2	8	-178.388	373.572	4.768	0.006	0.121	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009)	8	-178.426	373.647	4.843	0.005	0.121	0
Distance to nearest stream + Distance to nearest stream ^ 2 +	11	-175.094	373.671	4.867	0.005	0.137	0

Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat						
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2	8	-178.438	373.673	4.868	0.005	0.121	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009) + Elevation x % Urban (2009)	12	-174.09	373.943	5.138	0.005	0.142	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	11	-175.261	374.006	5.201	0.004	0.136	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009) + Elevation x Habitat	10	-176.501	374.231	5.427	0.004	0.13	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	12	-174.278	374.319	5.514	0.004	0.141	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 -	10	-176.548	374.326	5.522	0.004	0.13	0

2009) + % Regressive changes (1956 - 2009) ^ 2						
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009) + Elevation x Habitat	11	-175.508	374.5	5.695	0.003	0.135	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	11	-175.51	374.503	5.698	0.003	0.135	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + Elevation x Habitat	10	-176.65	374.529	5.725	0.003	0.129	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Urban (2009)	9	-177.774	374.548	5.743	0.003	0.124	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + Elevation x Habitat	10	-176.669	374.567	5.762	0.003	0.129	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Urban (2009)	9	-177.796	374.591	5.787	0.003	0.124	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009) + Elevation x % Urban (2009)	9	-177.801	374.601	5.797	0.003	0.124	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 -	10	-176.702	374.633	5.828	0.003	0.129	0

2009) + % Regressive changes (1956 - 2009) ^ 2							
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009)	10	-176.702	374.633	5.828	0.003	0.129	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x Habitat	12	-174.438	374.638	5.834	0.003	0.14	0
% Cropland (2009) + Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	12	-174.455	374.673	5.868	0.003	0.14	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	12	-174.483	374.73	5.925	0.003	0.14	0
% Cropland (2009) + Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009)	9	-177.868	374.736	5.932	0.003	0.123	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009) + Elevation x Habitat	12	-174.494	374.751	5.947	0.003	0.14	0

% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + Elevation x % Cropland (2009) + Elevation x Habitat	12	-174.497	374.757	5.953	0.003	0.14	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % Urban (2009) + Elevation x % Cropland (2009)	9	-177.884	374.767	5.963	0.003	0.123	0
Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009)	10	-176.773	374.775	5.97	0.003	0.129	0
% Cropland (2009) + Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Elevation x Habitat	10	-176.775	374.779	5.974	0.003	0.129	0
Distance to nearest road + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + Longitude + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2	10	-176.78	374.788	5.984	0.003	0.129	0
% Cropland (2009) + Distance to nearest stream + Distance to nearest stream ^ 2 + Elevation + Habitat + % No changes (1956 - 2009) + % No changes (1956 - 2009) ^ 2 + % Regressive changes (1956 - 2009) + % Regressive changes (1956 - 2009) ^ 2 + % Urban (2009)	12	-174.517	374.796	5.991	0.003	0.14	0

(b) Invasion success: area of occupancy

Model	df	logLik	AICc	delta	weight	R^2_{adj}	Pagel's λ
Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	8	-94.615	207.231	0	0.11	0.221	0

Minimum residence time + Native niche breadth	5	-98.459	207.719	0.488	0.086	0.177	0
Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time	9	-93.941	208.417	1.187	0.061	0.224	0
Introduction pathway + Minimum residence time + Native niche breadth	7	-96.74	209.015	1.785	0.045	0.19	0
Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time + Introduction pathway x Native niche breadth	11	-91.841	209.508	2.277	0.035	0.243	0
Minimum residence time + Native niche breadth + Vegetative reproduction	6	-98.256	209.647	2.417	0.033	0.17	0
Introduction pathway + Minimum residence time + Vegetative reproduction + Introduction pathway x Minimum Residence Time	9	-94.587	209.709	2.479	0.032	0.211	0
Height + Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	9	-94.613	209.761	2.531	0.031	0.211	0
Introduction pathway + Minimum residence time	6	-98.343	209.822	2.591	0.03	0.168	0
Dispersal syndrome + Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	10	-93.438	210.019	2.788	0.027	0.223	0
Height + Minimum residence time + Native niche breadth	6	-98.459	210.054	2.823	0.027	0.166	0
Dispersal syndrome + Minimum residence time + Native niche breadth	7	-97.558	210.649	3.419	0.02	0.174	0
Height + Introduction pathway + Minimum residence time + Native niche breadth	8	-96.411	210.823	3.592	0.018	0.186	0
Height + Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time	10	-93.851	210.844	3.614	0.018	0.215	0
Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction	10	-93.916	210.975	3.744	0.017	0.214	0

+ Introduction pathway x Minimum Residence Time							
Dispersal syndrome + Introduction pathway + Minimum residence time + Native niche breadth	9	-95.314	211.164	3.933	0.015	0.197	0
Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction	8	-96.599	211.198	3.967	0.015	0.182	0
Height + Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time + Introduction pathway x Native niche breadth	12	-91.352	211.292	4.062	0.014	0.241	0
Dispersal syndrome + Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time	11	-92.75	211.325	4.095	0.014	0.225	0
Growth form + Minimum residence time + Native niche breadth	7	-98.001	211.536	4.306	0.013	0.165	0
Dispersal syndrome + Introduction pathway + Minimum residence time	8	-96.858	211.715	4.484	0.012	0.177	0
Growth form + Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	10	-94.324	211.791	4.561	0.011	0.206	0
Introduction pathway + Minimum residence time + Vegetative reproduction	7	-98.154	211.842	4.611	0.011	0.161	0
Height + Minimum residence time + Native niche breadth + Vegetative reproduction	7	-98.253	212.041	4.81	0.01	0.159	0
Height + Introduction pathway + Minimum residence time	7	-98.285	212.104	4.873	0.01	0.159	0
Minimum residence time	4	-101.825	212.176	4.946	0.009	0.117	0
Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction + Introduction pathway x Minimum Residence Time + Introduction pathway x Native niche breadth	12	-91.824	212.237	5.006	0.009	0.232	0
Height + Introduction pathway + Minimum residence time + Vegetative reproduction + Introduction pathway x Minimum Residence Time	10	-94.586	212.315	5.084	0.009	0.201	0

Growth form + Minimum residence time	6	-99.619	212.374	5.143	0.008	0.142	0
Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Native niche breadth	9	-95.974	212.483	5.252	0.008	0.184	0
Height + Introduction pathway + Minimum residence time + Introduction pathway x Height + Introduction pathway x Minimum Residence Time	11	-93.408	212.642	5.411	0.007	0.213	0
Dispersal syndrome + Height + Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	11	-93.412	212.65	5.419	0.007	0.213	0
Dispersal syndrome + Introduction pathway + Minimum residence time + Vegetative reproduction + Introduction pathway x Minimum Residence Time	11	-93.428	212.681	5.451	0.007	0.212	0
Dispersal syndrome + Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time + Introduction pathway x Native niche breadth	13	-90.704	212.842	5.611	0.007	0.242	0
Dispersal syndrome + Height + Minimum residence time + Native niche breadth	8	-97.498	212.997	5.766	0.006	0.164	0
Dispersal syndrome + Minimum residence time + Native niche breadth + Vegetative reproduction	8	-97.499	212.999	5.768	0.006	0.164	0
Growth form + Minimum residence time + Native niche breadth + Vegetative reproduction	8	-97.571	213.141	5.911	0.006	0.162	0
Height + Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction	9	-96.327	213.19	5.959	0.006	0.177	0

(c) Invasion success: habitat range

Model	df	logLik	AICc	delta	weight	R^2_{adj}	Pagel's λ
Minimum residence time + Native niche breadth	5	-66.825	144.451	0	0.13	0.12	0.279

Introduction pathway + Minimum residence time	6	-66.361	145.857	1.406	0.064	0.13	0
Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	8	-63.961	145.922	1.472	0.062	0.158	0
Minimum residence time	4	-69.012	146.55	2.099	0.046	0.094	0
Introduction pathway + Minimum residence time + Native niche breadth	7	-65.563	146.66	2.21	0.043	0.136	0
Height + Minimum residence time + Native niche breadth	6	-66.763	146.662	2.211	0.043	0.11	0.305
Minimum residence time + Native niche breadth + Vegetative reproduction	6	-66.776	146.686	2.235	0.043	0.11	0.272
Growth form + Minimum residence time	6	-67.3	147.735	3.284	0.025	0.109	0
Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time	9	-63.622	147.779	3.328	0.025	0.154	0
Height + Introduction pathway + Minimum residence time	7	-66.282	148.098	3.648	0.021	0.12	0
Introduction pathway + Minimum residence time + Vegetative reproduction	7	-66.343	148.22	3.769	0.02	0.119	0
Height + Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	9	-63.849	148.233	3.782	0.02	0.149	0
Height + Minimum residence time	5	-68.746	148.291	3.84	0.019	0.089	0
Introduction pathway + Minimum residence time + Vegetative reproduction + Introduction pathway x Minimum Residence Time	9	-63.913	148.362	3.911	0.018	0.148	0
Height + Introduction pathway + Minimum residence time + Native niche breadth	8	-65.297	148.594	4.143	0.016	0.13	0
Growth form + Height + Minimum residence time	7	-66.607	148.749	4.298	0.015	0.102	0.298
Minimum residence time + Vegetative reproduction	5	-69.012	148.824	4.373	0.015	0.083	0
Growth form + Minimum residence time + Native niche breadth	7	-66.683	148.901	4.45	0.014	0.111	0
Height + Minimum residence time + Native niche breadth + Vegetative reproduction	7	-66.701	148.936	4.485	0.014	0.1	0.297
Growth form + Height + Minimum residence time + Native niche breadth	8	-65.508	149.015	4.564	0.013	0.116	0.358

Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction	8	-65.53	149.059	4.608	0.013	0.125	0
Dispersal syndrome + Introduction pathway + Minimum residence time	8	-65.561	149.121	4.67	0.013	0.124	0
Dispersal syndrome + Minimum residence time + Native niche breadth	7	-66.828	149.191	4.74	0.012	0.108	0
Native niche breadth	4	-70.438	149.402	4.951	0.011	0.051	0.321
Height + Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Minimum Residence Time	10	-63.154	149.45	4.999	0.011	0.141	0.287
Dispersal syndrome + Introduction pathway + Minimum residence time + Introduction pathway x Minimum Residence Time	10	-63.272	149.686	5.235	0.009	0.15	0
Dispersal syndrome + Introduction pathway + Minimum residence time + Native niche breadth	9	-64.707	149.949	5.499	0.008	0.131	0
Growth form + Introduction pathway + Minimum residence time	8	-66.037	150.074	5.623	0.008	0.114	0
Growth form + Minimum residence time + Vegetative reproduction	7	-67.293	150.121	5.67	0.008	0.098	0
Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction + Introduction pathway x Minimum Residence Time	10	-63.57	150.282	5.831	0.007	0.143	0

(d) Invasion success: invaded climatic niche breadth

Model	df	logLik	AICc	delta	weight	R^2_{adj}	Pagel's λ
Minimum residence time	4	-120.804	250.135	0	0.154	0.103	0
Minimum residence time + Native niche breadth	5	-119.823	250.445	0.31	0.132	0.113	0
Introduction pathway + Minimum residence time	6	-119.344	251.823	1.688	0.066	0.112	0
Height + Minimum residence time	5	-120.58	251.96	1.824	0.062	0.096	0
Minimum residence time + Vegetative reproduction	5	-120.648	252.096	1.961	0.058	0.095	0
Minimum residence time + Native niche breadth + Vegetative reproduction	6	-119.74	252.616	2.481	0.045	0.103	0

Height + Minimum residence time + Native niche breadth	6	-119.803	252.741	2.606	0.042	0.102	0
Introduction pathway + Minimum residence time + Native niche breadth	7	-119.022	253.579	3.444	0.028	0.107	0
Growth form + Minimum residence time	6	-120.234	253.602	3.467	0.027	0.092	0
Height + Minimum residence time + Vegetative reproduction	6	-120.387	253.909	3.774	0.023	0.089	0
Introduction pathway + Minimum residence time + Vegetative reproduction	7	-119.31	254.155	4.02	0.021	0.101	0
Height + Introduction pathway + Minimum residence time	7	-119.33	254.194	4.059	0.02	0.101	0
Dispersal syndrome + Minimum residence time	6	-120.64	254.415	4.28	0.018	0.083	0
Height + Introduction pathway + Minimum residence time + Introduction pathway x Height	9	-117.016	254.568	4.433	0.017	0.128	0
Dispersal syndrome + Minimum residence time + Native niche breadth	7	-119.534	254.602	4.466	0.017	0.096	0
Introduction pathway + Minimum residence time + Native niche breadth + Introduction pathway x Native niche breadth	9	-117.05	254.635	4.5	0.016	0.127	0
Height + Minimum residence time + Native niche breadth + Vegetative reproduction	7	-119.707	254.949	4.814	0.014	0.092	0
Growth form + Minimum residence time + Native niche breadth	7	-119.73	254.994	4.859	0.014	0.092	0
Growth form + Minimum residence time + Vegetative reproduction	7	-120.064	255.661	5.526	0.01	0.084	0
Introduction pathway + Minimum residence time + Native niche breadth + Vegetative reproduction	8	-118.999	255.997	5.862	0.008	0.096	0
Growth form + Height + Minimum residence time	7	-120.232	255.999	5.864	0.008	0.08	0
Height + Introduction pathway + Minimum residence time + Native niche breadth	8	-119.022	256.044	5.909	0.008	0.095	0
Dispersal syndrome + Introduction pathway + Minimum residence time	8	-119.025	256.049	5.914	0.008	0.095	0

Table S2.6. Model-averaged coefficients (with 95% confidence intervals) of binomial GLMs that related the proportion of gardening plants to environmental variables. The intercept was the mean proportion of gardening plants when all numerical explanatory variables are at their mean value, for the reference levels of: cropland habitat. N = 190 invaded plots.

Variable	Model-averaged coefficients without interactions (95% confidence interval)	Model-averaged coefficients with interactions (95% confidence interval)
Intercept	-1.49 (-2.085, -0.896)	-1.363 (-1.991, -0.735)
Distance to nearest stream (linear)	0.068 (-0.404, 0.539)	0.098 (-0.389, 0.584)
Dist. to nearest stream (quadratic)	0.079 (-0.058, 0.216)	0.079 (-0.06, 0.219)
Elevation	0.325 (0.08, 0.571)	0.134 (-0.321, 0.59)
Habitat (Natural)	1.527 (0.858, 2.196)	1.474 (0.795, 2.153)
Habitat (Urban)	0.83 (0.099, 1.56)	0.706 (-0.049, 1.461)
% Regressive changes (1956-2009) (linear)	-0.011 (-0.278, 0.255)	0 (-0.303, 0.304)
% Regressive changes (1956-2009) (quadratic)	-0.095 (-0.393, 0.203)	-0.15 (-0.522, 0.222)
% No changes (1956-2009) (linear)	-0.047 (-0.283, 0.189)	-0.093 (-0.423, 0.237)
% No changes (1956-2009) (quadratic)	0.027 (-0.189, 0.244)	0.055 (-0.198, 0.308)
% Cropland land-cover (2009)	-0.042 (-0.24, 0.155)	-0.053 (-0.27, 0.164)
Longitude	0.014 (-0.099, 0.127)	0.008 (-0.08, 0.097)
% Urban land-cover (2009)	-0.009 (-0.161, 0.143)	-0.008 (-0.172, 0.156)
Distance to nearest road	0.005 (-0.1, 0.11)	0.001 (-0.076, 0.078)
Elevation x Habitat (Natural)		0.397 (-0.238, 1.032)
Elevation x Habitat (Urban)		0.018 (-0.62, 0.657)
Elevation x % Cropland land-cover (2009)		-0.002 (-0.083, 0.08)
Elevation x % Urban land-cover (2009)		-0.007 (-0.1, 0.086)

Table S2.7. Coefficients (model-averaged) for the PGLS modelling invasion success, measured through the area of occupancy (calculated on a 10-km grid), habitat range, and invaded climatic niche breadth (all three were log-transformed). The intercept was the mean invasion success when all numerical explanatory variables are at their mean value, for the reference levels of: introduced through agriculture and forestry, dispersal through animals, growth form as annual forb and grass, and vegetative reproduction absent. Numerical predictors were standardised. N = 81 (77 non-native plants, four duplicated since they were introduced through two pathways). Abbreviations: Intro. pathway = Introduction pathway, Unint. = Unintentional.

Model	Variable	Model-averaged coefficients without interactions (95% confidence interval)	Model-averaged coefficients with interactions (95% confidence interval)
Area of occupancy (10-km, log-transformed)	Intercept	0.793 (0.259, 1.326)	0.632 (0.067, 1.196)
	Intro. pathway (Gardening)	0.085 (-0.356, 0.526)	0.131 (-0.476, 0.738)
	Intro. pathway (Unintentional)	0.247 (-0.463, 0.956)	0.549 (-0.153, 1.251)
	Minimum residence time (MRT)	0.297 (0.11, 0.483)	0.155 (-0.311, 0.62)
	Native niche breadth	0.174 (-0.077, 0.426)	0.11 (-0.309, 0.528)
	Height	0.005 (-0.096, 0.107)	0.002 (-0.125, 0.13)
	Dispersal (Unspecific)	-0.022 (-0.224, 0.181)	-0.023 (-0.225, 0.178)
	Dispersal (Wind)	0.031 (-0.221, 0.283)	0.026 (-0.209, 0.262)
	Growth form (Perennial forbs & grasses)	-0.004 (-0.152, 0.144)	0 (-0.079, 0.08)
	Growth form (Shrubs & trees)	-0.021 (-0.24, 0.198)	-0.004 (-0.109, 0.101)
	Vegetative reproduction (Present)	-0.025 (-0.23, 0.179)	-0.005 (-0.164, 0.155)
	Intro. pathway (Gardening) : MRT		0.034 (-0.48, 0.548)
	Intro. pathway (Unintentional) : MRT		0.588 (-0.041, 1.217)
	Intro. pathway (Gardening) : Native niche breadth		-0.045 (-0.37, 0.279)
	Intro. pathway (Unint.) : Native niche breadth		-0.103 (-0.628, 0.423)
	Intro. pathway (Gardening) : Height		0.005 (-0.092, 0.102)
	Intro. pathway (Unintentional) : Height		0.028 (-0.567, 0.622)
	Intercept	0.484 (0.003, 0.964)	0.297 (-0.102, 0.695)

Model	Variable	Model-averaged coefficients without interactions (95% confidence interval)	Model-averaged coefficients with interactions (95% confidence interval)
Habitat range (log-transformed)	Intro. pathway (Gardening)	0.083 (-0.248, 0.413)	0.24 (-0.17, 0.649)
	Intro. pathway (Unintentional)	0.147 (-0.332, 0.627)	0.434 (-0.002, 0.87)
	Minimum residence time (MRT)	0.178 (0.043, 0.313)	0.263 (-0.053, 0.579)
	Native niche breadth	0.068 (-0.084, 0.22)	0.017 (-0.076, 0.11)
	Height	0.009 (-0.085, 0.103)	0.009 (-0.068, 0.086)
	Dispersal (Unspecific)	-0.007 (-0.099, 0.085)	-0.008 (-0.104, 0.088)
	Dispersal (Wind)	0.001 (-0.083, 0.086)	0.002 (-0.089, 0.093)
	Growth form (Perennial forbs & grasses)	-0.007 (-0.136, 0.122)	
	Growth form (Shrubs & trees)	-0.038 (-0.284, 0.207)	
	Vegetative reproduction (Present)	0.005 (-0.108, 0.119)	0.007 (-0.102, 0.115)
	Intro. pathway (Gardening) : MRT		-0.17 (-0.522, 0.182)
	Intro. pathway (Unintentional) : MRT		0.14 (-0.272, 0.551)
Invaded climatic niche breadth (log-transformed)	Intercept	-0.966 (-1.399, -0.534)	-0.72 (-1.534, 0.094)
	Intro. pathway (Gardening)	-0.046 (-0.445, 0.354)	-0.473 (-1.385, 0.439)
	Intro. pathway (Unintentional)	0.038 (-0.366, 0.442)	-0.205 (-2.225, 1.814)
	Minimum residence time (MRT)	0.37 (0.127, 0.613)	0.354 (0.103, 0.605)
	Native niche breadth	0.061 (-0.157, 0.28)	0.369 (-0.534, 1.272)
	Height	-0.012 (-0.146, 0.123)	-0.211 (-0.736, 0.313)
	Dispersal (Unspecific)	-0.01 (-0.17, 0.15)	
	Dispersal (Wind)	-0.003 (-0.167, 0.162)	
	Growth form (Perennial forbs & grasses)	-0.006 (-0.187, 0.176)	
	Growth form (Shrubs & trees)	-0.02 (-0.258, 0.217)	
	Vegetative reproduction (Present)	-0.026 (-0.281, 0.229)	
	Intro. pathway (Gardening) : Native niche breadth		-0.323 (-1.191, 0.545)

Model	Variable	Model-averaged coefficients without interactions (95% confidence interval)	Model-averaged coefficients with interactions (95% confidence interval)
	Intro. pathway (Unint.) : Native niche breadth		-0.42 (-1.457, 0.617)
	Intro. pathway (Gardening) : Height		0.303 (-0.407, 1.012)
	Intro. pathway (Unintentional) : Height		-0.156 (-3.24, 2.928)

Table S2.8. Pairwise covariation among all plant attributes. The effect size metric and the significance test were appropriate to each categorical x continuous combination (see Supplementary Methods). Trait covariations were sorted by decreasing order of effect size (in absolute value). Significant trait associations were highlighted in bold. N = 81 (77 non-native plants, four duplicated since they were introduced through two pathways).

Variable 1	Variable 2	Combination	Effect size metric	Effect size value	Significance test	Significance (p.v)
Growth form	Vegetative reproduction	categorical x categorical	Cramér's V	**0.604**	Chi-square	**0.000**
Height	Growth form	continuous x categorical	Eta squared	**0.519**	ANOVA	**0.000**
Introduction pathway	Growth form	categorical x categorical	Cramér's V	**0.437**	Chi-square	**0.000**
Native niche breadth	Height	continuous x continuous	Pearson's correlation	**-0.365**	t-test	**0.001**
Native niche breadth	Growth form	continuous x categorical	Eta squared	**0.293**	ANOVA	**0.000**
Dispersal	Vegetative reproduction	categorical x categorical	Cramér's V	0.245	Chi-square	0.088
Dispersal	Growth form	categorical x categorical	Cramér's V	0.230	Chi-square	0.073
Height	Introduction pathway	continuous x categorical	Eta squared	**0.222**	ANOVA	**0.000**
Introduction pathway	Vegetative reproduction	categorical x categorical	Cramér's V	0.192	Chi-square	0.224
Minimum residence time	Height	continuous x continuous	Pearson's correlation	-0.181	t-test	0.105
Native niche breadth	Introduction pathway	continuous x categorical	Eta squared	**0.174**	ANOVA	**0.001**
Introduction pathway	Dispersal	categorical x categorical	Cramér's V	0.153	Chi-square	0.432
Minimum residence time	Native niche breadth	continuous x continuous	Pearson's correlation	0.144	t-test	0.200
Height	Dispersal	continuous x categorical	Eta squared	0.068	ANOVA	0.064
Minimum residence time	Growth form	continuous x categorical	Eta squared	0.059	ANOVA	0.092

Variable 1	Variable 2	Combination	Effect size metric	Effect size value	Significance test	Significance (p.v)
Native niche breadth	Dispersal	continuous x categorical	Eta squared	0.027	ANOVA	0.339
Minimum residence time	Introduction pathway	continuous x categorical	Eta squared	0.021	ANOVA	0.435
Minimum residence time	Dispersal	continuous x categorical	Eta squared	0.020	ANOVA	0.451
Native niche breadth	Vegetative reproduction	continuous x categorical	Eta squared	0.014	ANOVA	0.297
Height	Vegetative reproduction	continuous x categorical	Eta squared	0.007	ANOVA	0.473
Minimum residence time	Vegetative reproduction	continuous x categorical	Eta squared	0.000	ANOVA	0.859

Supplementary figures

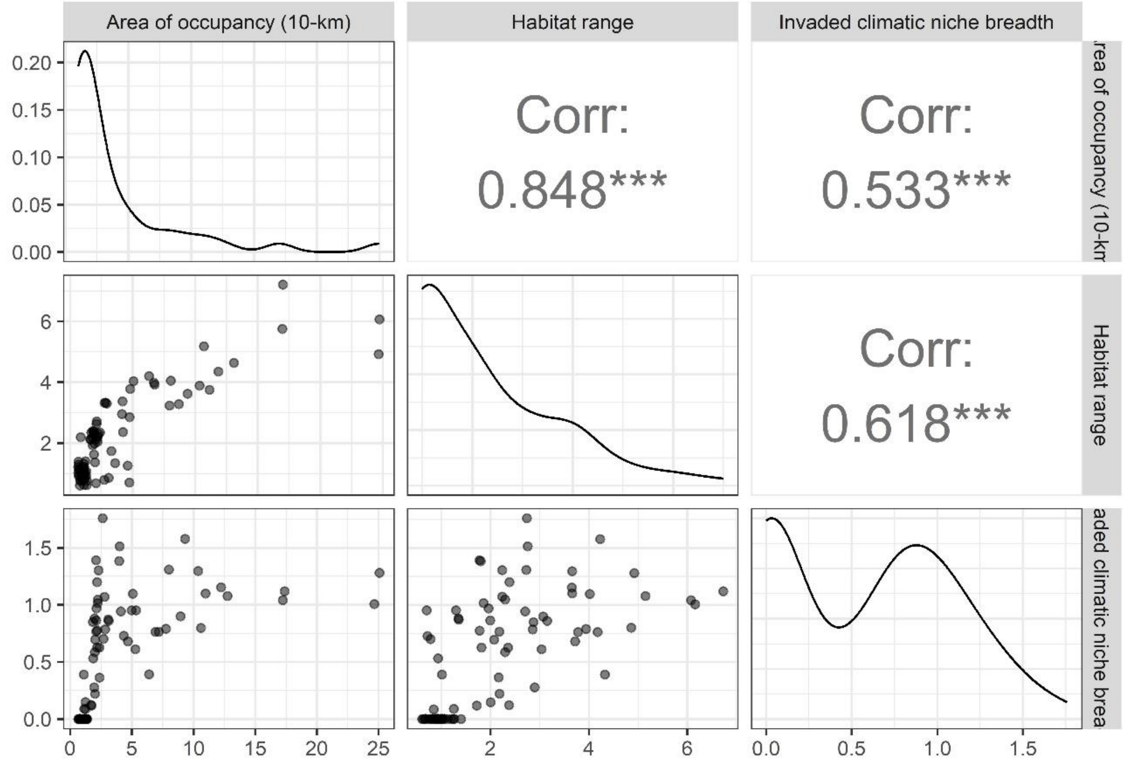
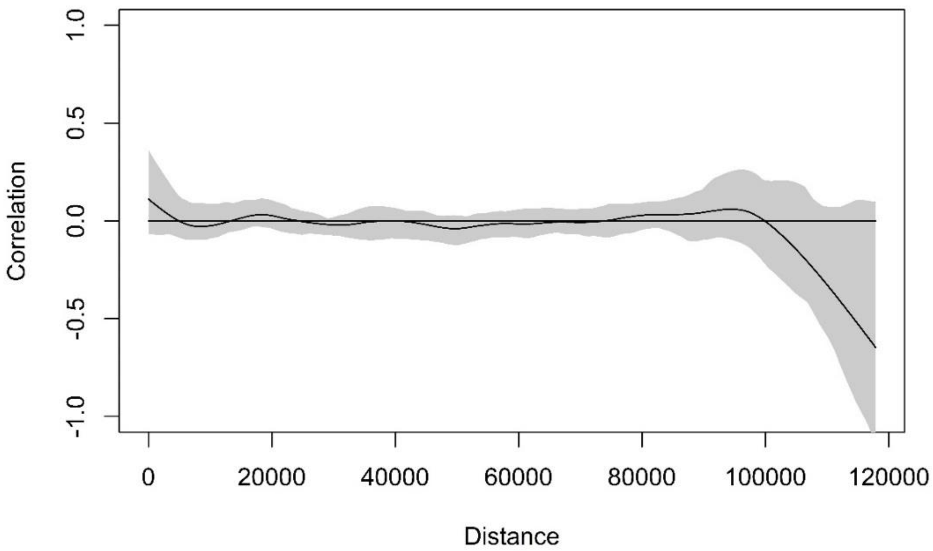


Fig. S2.1. Correlation among area of occupancy (calculated on a 10-km grid), habitat range, and invaded climatic niche breadth. Lower-left panels showed scatterplot (transparency and jittering added for visualization), upper-right panel was Pearson's correlation, main diagonal showed smoothed histograms. N = 81 (77 non-native plants, four duplicated since they were introduced through two pathways).


a) Model without interactions

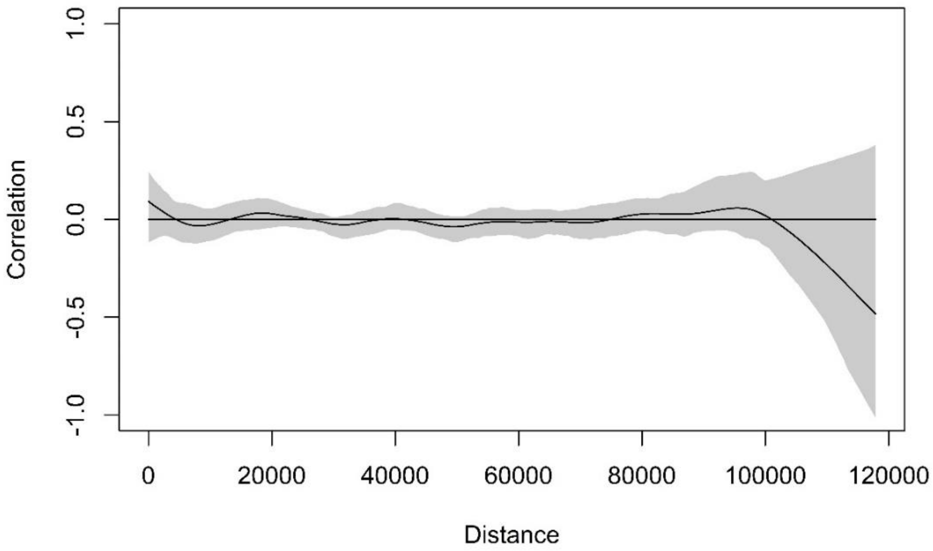
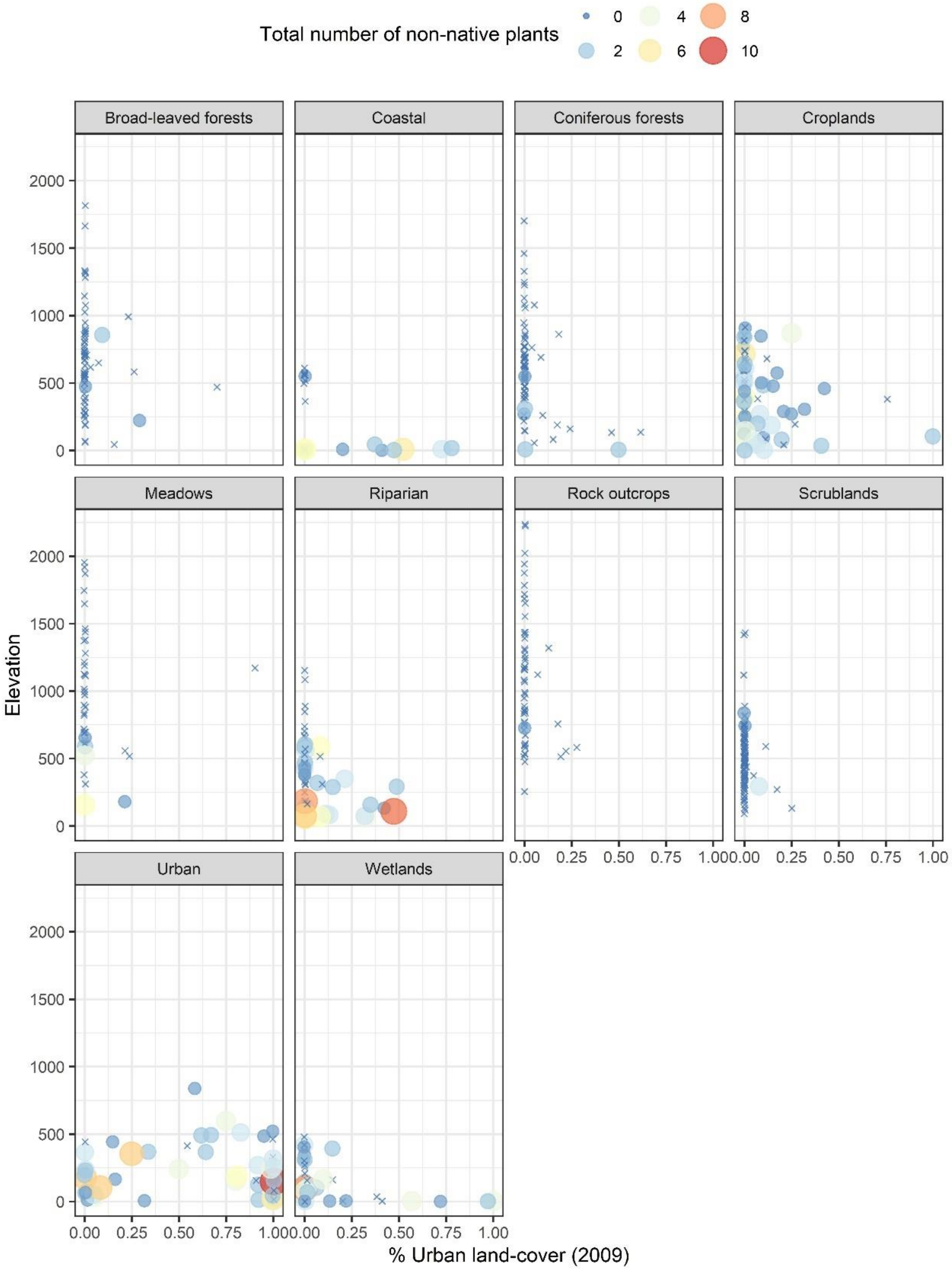

b) Model with interactions

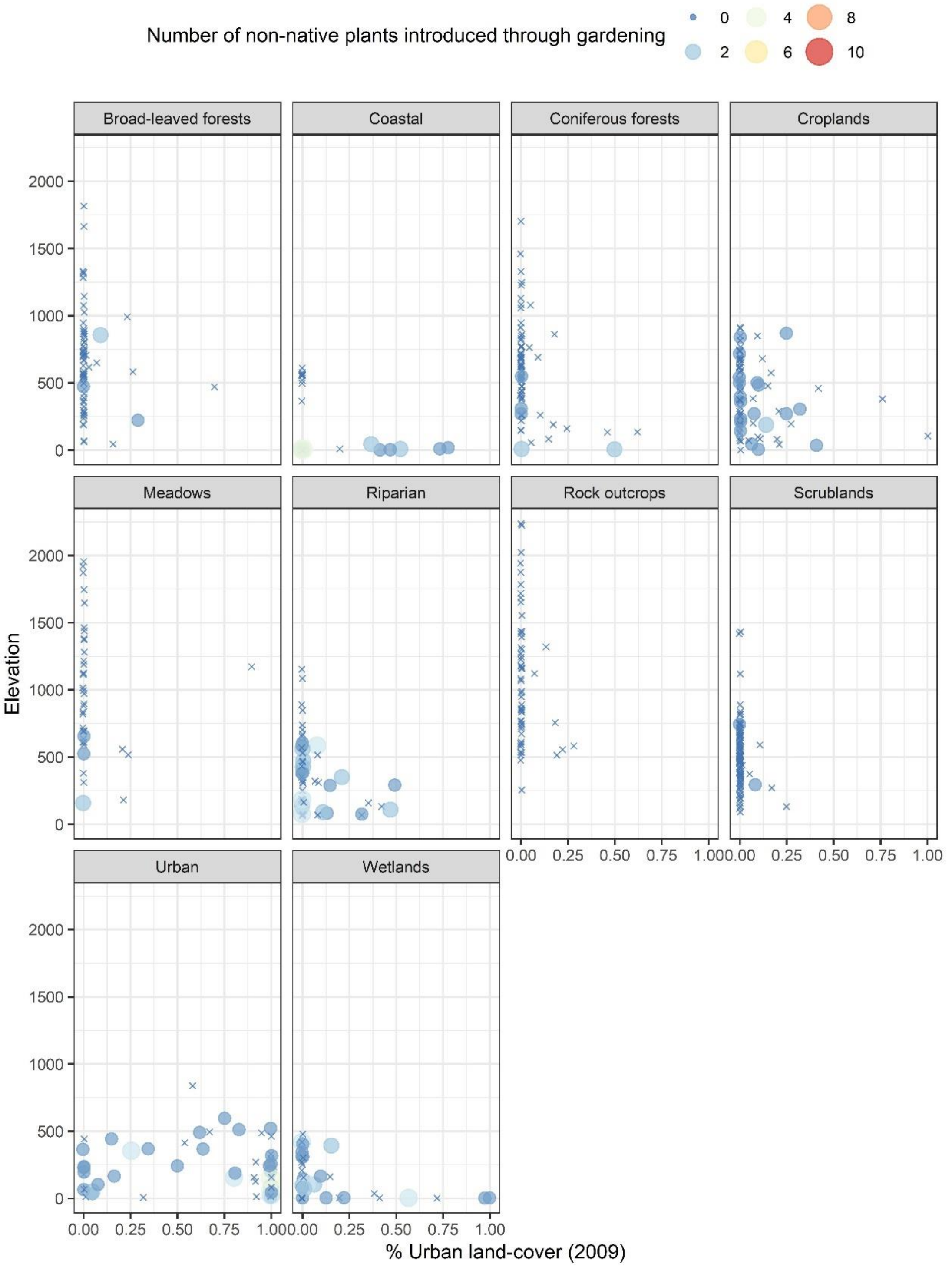
Fig. S2.2. Spline correlograms of the deviance residuals (N = 190 residuals), from the GLM binomial models of proportion of plants introduced through gardening: a) without interactions, and b) with interactions. Both models were "full models", in the sense they included all main effects. The units in the x-axis (Distance) were meters, the y-axis was Moran's **I**. The bootstrap confidence intervals overlapped 0, suggesting no spatial autocorrelation (i.e. Moran's **I** was not different from 0). We generated a 95% confidence interval through bootstrap (with 100 resamples).

a)



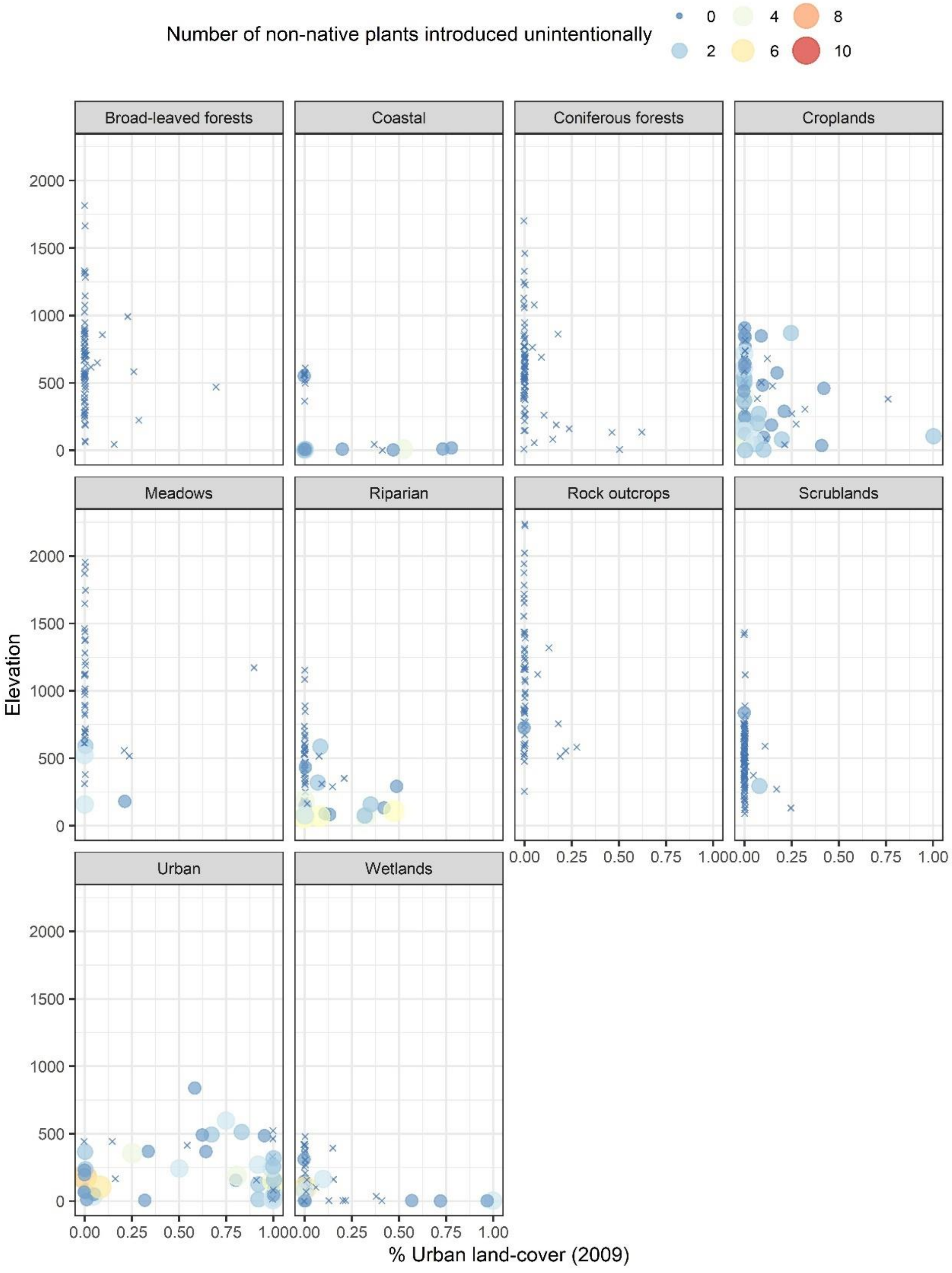
Total number of non-native plants
0
2
4
6
8
10
Broad-leaved forests
Coastal
Coniferous forests
Croplands
Meadows
Riparian
Rock outcrops
Scrublands
Urban
Wetlands
Elevation
0
500
1000
1500
2000
0.00
0.25
0.50
0.75
1.00
% Urban land-cover (2009)

b)



Number of non-native plants introduced through gardening
0
2
4
6
8
10
Broad-leaved forests
Coastal
Coniferous forests
Croplands
Meadows
Riparian
Rock outcrops
Scrublands
Urban
Wetlands
Elevation
0
500
1000
1500
2000
0.00
0.25
0.50
0.75
1.00
% Urban land-cover (2009)

c)


Number of non-native plants introduced unintentionally
0
2
4
6
8
10
Broad-leaved forests
Coastal
Coniferous forests
Croplands
Meadows
Riparian
Rock outcrops
Scrublands
Urban
Wetlands
2000
1500
1000
500
0
Elevation
0.00
0.25
0.50
0.75
1.00
% Urban land-cover (2009)

d)

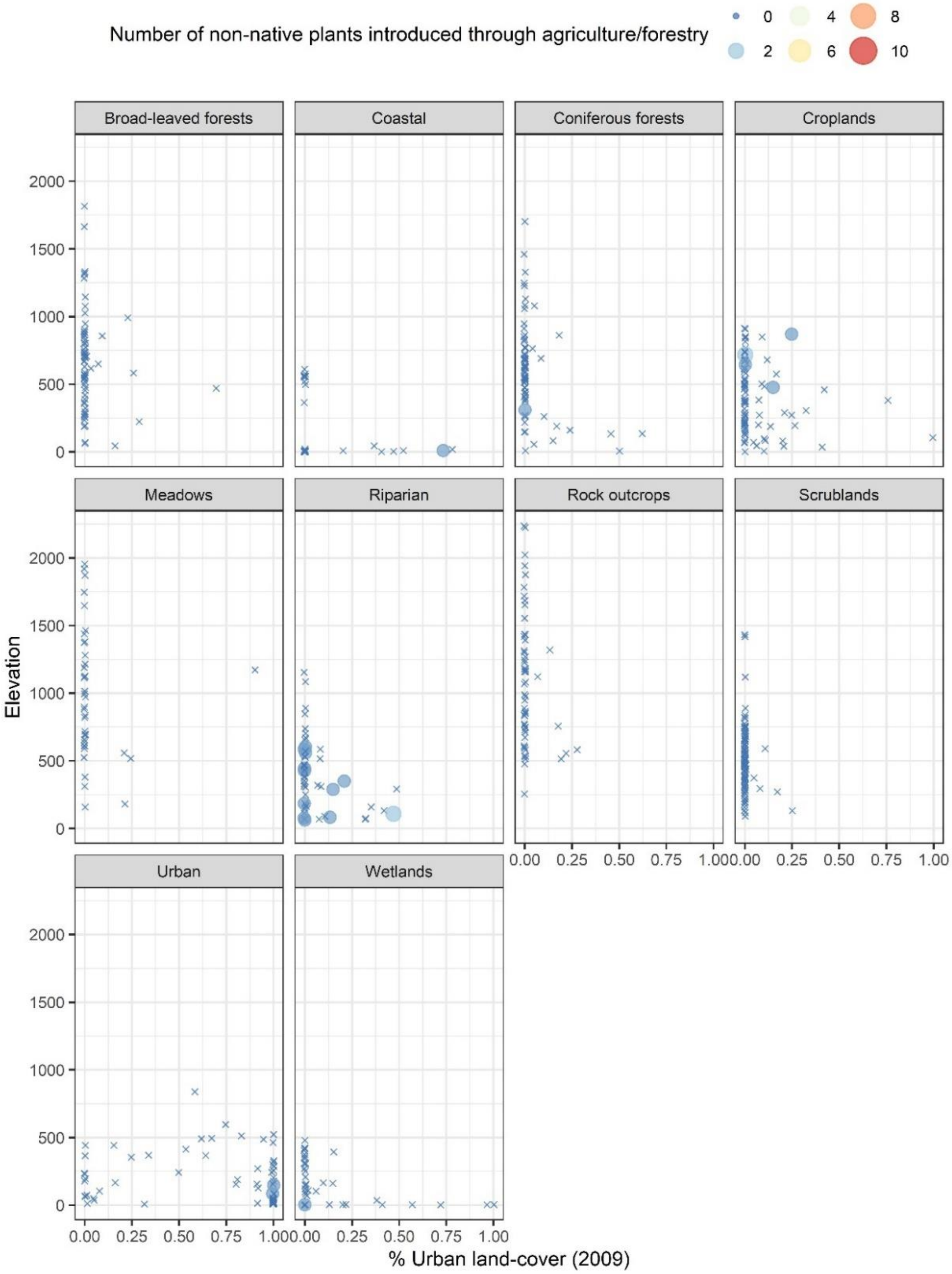
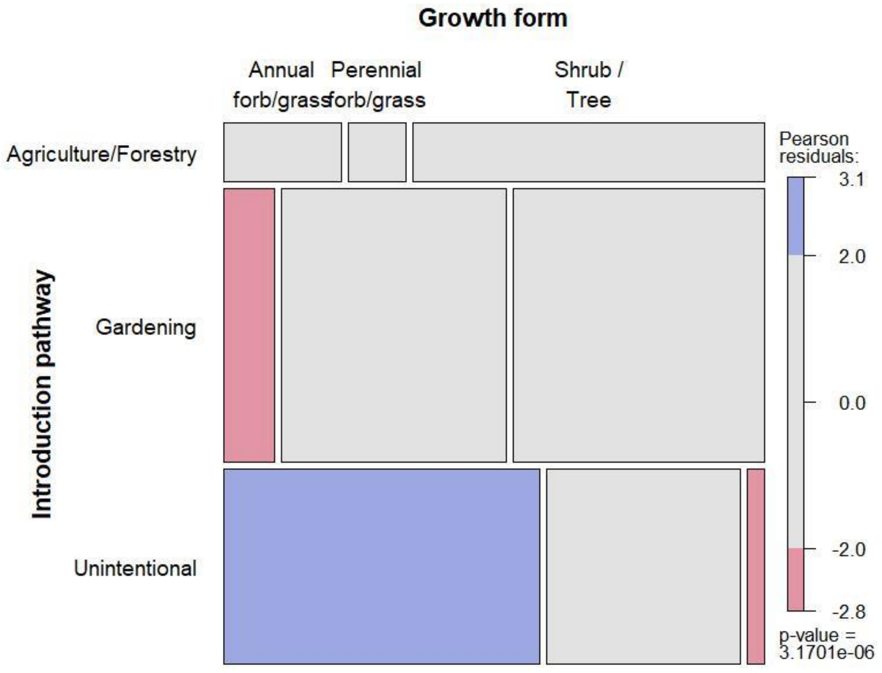
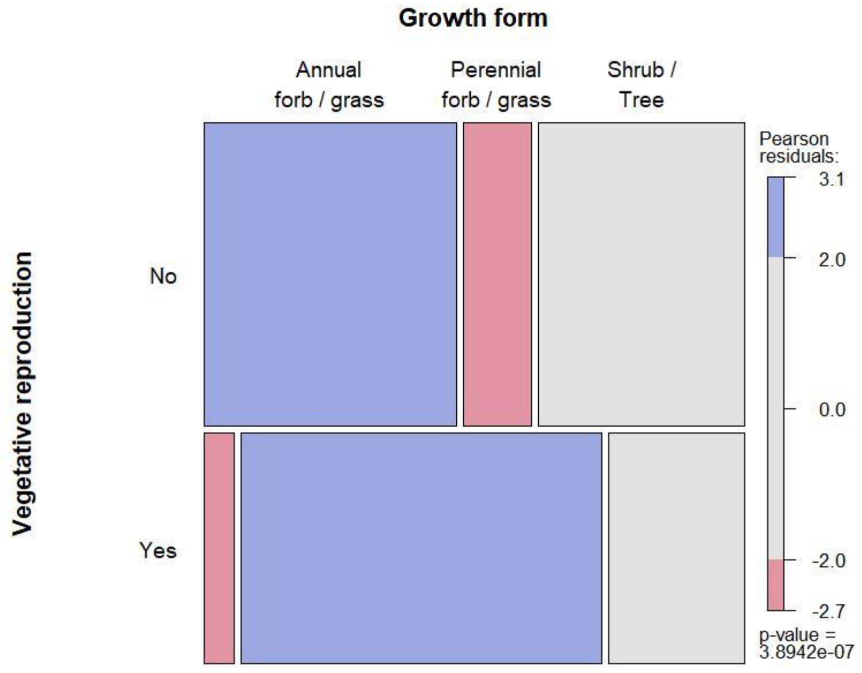


Fig. S2.3. Number of non-native plants per plot, in relationship to elevation and urban land-cover, for each of the ten habitat types, considering: a) all non-native plants, b) plants introduced through gardening, c) plants introduced unintentionally, d) plants introduced through agriculture/forestry. Circles represented invaded plots, which increase in size and turn into warmer colours with increasing number of non-native plants. Crosses indicate non-invaded plots. Random noise (jittering) and transparency were added for visualization. N = 632 plots.

a)


Growth form
Annual forb/grass
Perennial forb/grass
Shrub / Tree
Agriculture/Forestry
Gardening
Unintentional
Introduction pathway
Pearson residuals:
3.1
2.0
0.0
-2.0
-2.8
p-value = 3.1701e-06

b)


Growth form
Annual forb / grass
Perennial forb / grass
Shrub / Tree
No
Yes
Vegetative reproduction
Pearson residuals:
3.1
2.0
0.0
-2.0
-2.7
p-value = 3.8942e-07

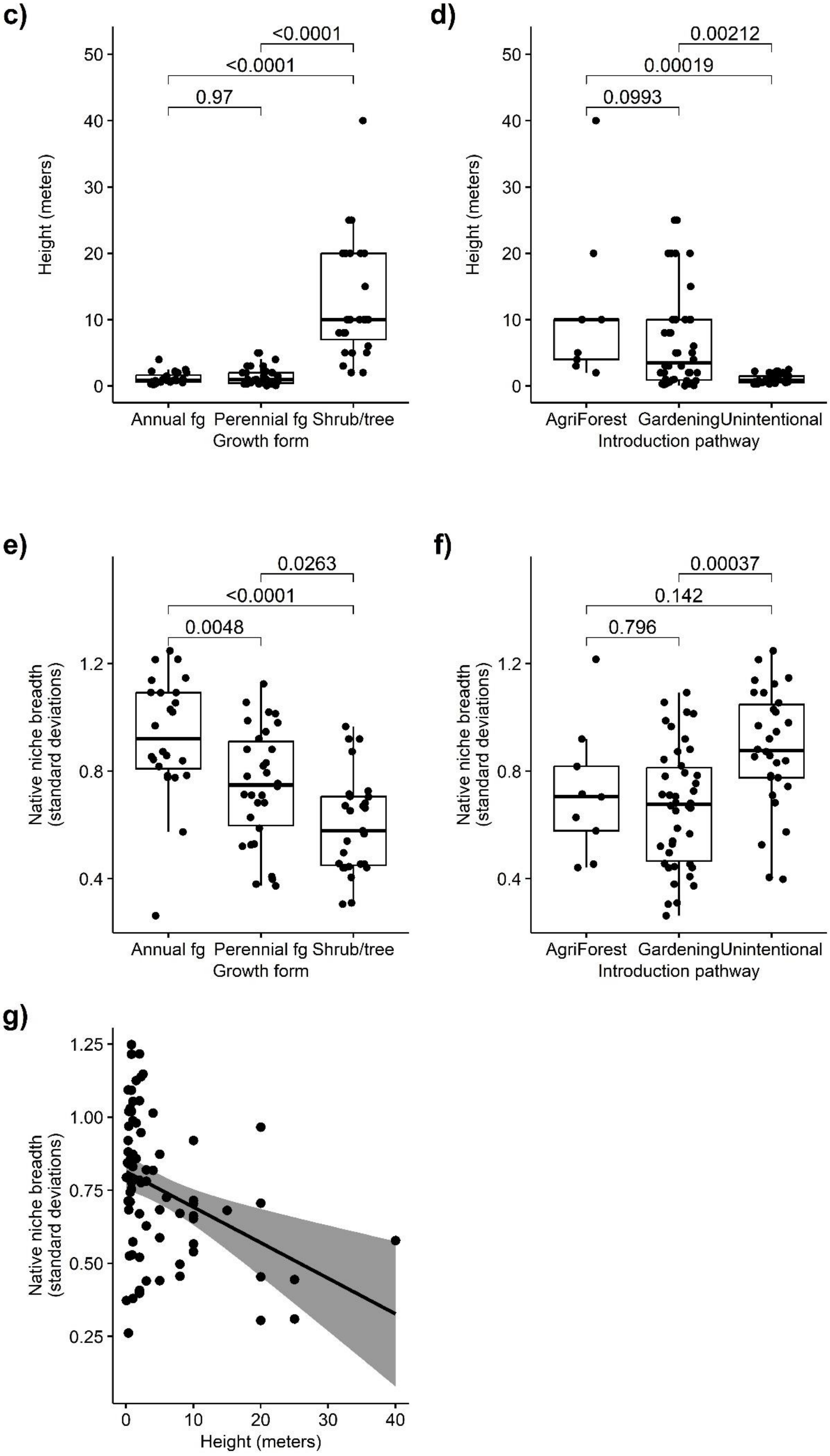

c)
<0.0001
<0.0001
0.97
Height (meters)
50
40
30
20
10
0
Annual fg
Perennial fg
Shrub/tree
Growth form
d)
0.00212
0.00019
0.0993
Height (meters)
50
40
30
20
10
0
AgriForest
Gardening
Unintentional
Introduction pathway
e)
0.0263
<0.0001
0.0048
Native niche breadth (standard deviations)
1.2
0.8
0.4
Annual fg
Perennial fg
Shrub/tree
Growth form
f)
0.00037
0.142
0.796
Native niche breadth (standard deviations)
1.2
0.8
0.4
AgriForest
Gardening
Unintentional
Introduction pathway
g)
Native niche breadth (standard deviations)
1.25
1.00
0.75
0.50
0.25
0
10
20
30
40
Height (meters)

Fig. S2.4. Covariation among introduction pathways and minimum residence time and plant traits. a)**-**b) Covariation between introduction pathways and growth form, and between growth form and vegetative reproduction, shown through mosaic plots. Tiles in blue indicated overrepresentation of non-native plants for that combination of categories, while red indicated underrepresentation (see Appendix 2 Supplementary methods). C)-f) Covariation between growth form and introduction pathway with height and native niche breadth, shown through boxplots. Numbers indicated significance of pairwise Tukey contrasts. G) Covariation between height and native niche breadth, shown through a scatterplot. Dots depicted non-native plants, with jittering (random noise) and transparency added for visualization. See Table S2.8 for effect size and significance of all pairwise trait covariations. N = 81 (77 non-native plants, four duplicated since they were introduced through two pathways).

Supplementary discussion

Correlation among plant traits

Annual plants rarely reproduced vegetatively (only 8% of annuals reproduced vegetatively: 2 out of 24), tended to be shorter than shrubs and trees (around ten meters difference, on average, similar result for perennial herbaceous plants), and tended to have wider native niches compared to all other growth forms (0.19 standard deviation difference with perennial grasses, and 0.33 standard deviation difference with shrubs and trees, on average). Taller plants tended to have narrower native niches (Pearson's correlation = - 0.37).

The invaded niche of non-native plants introduced through agriculture and forestry

We focused on habitat type to describe pathway-specific differences in the invaded niche between agriculture/forestry plants and the rest of non-native plants, since this variable was the main correlate of pathway-specific differences in the invaded niche between gardening and unintentional plants (main text).

Non-native plants introduced through agriculture and forestry were infrequent invaders (N = 20 invaded plots), and were mostly invaders of riparian habitats (60%: 12 out of 20 invaded plots). More rarely, they invaded croplands (15%: 3 out of 20), and urban habitats (10%: 2 out of 20). The following habitats were represented by a single invaded plot: coastal, coniferous forests and wetlands.

Non-native plants introduced through agriculture and forestry were a minority of invaders (on average, less than 15% of all invaders, across all habitat types). The habitat that promoted invasion by agriculture and forestry plants the most was the riparian habitat: on average, 13% of all invaders in a plot.

The importance of the riparian habitat for agriculture and forestry plants probably relates to waterways acting as dispersal corridors for propagules originating in croplands and forestry plantings located close to rivers (Kalusová et al., 2023; Wagner et al., 2017). In comparison, croplands did not promote invasion by agriculture and forestry plants, possibly due to the inclusion of forestry plants (i.e. if agricultural introductions were numerous enough to be assessed separately, invasion patterns could change).

Pathway-specific niche differences in relationship to rarely invaded natural habitats

We found pathway-specific differences in relationship to natural habitats represented by five or less invaded plots (Table 3.3 in the main text). We suggest here some tentative explanations for the pathway-specific differences, keeping in mind that the small sample size might yield unrepresentative results.

Plants introduced through gardening were the sole invaders in forests (broad-leaved and coniferous), which could be related to trait selection. In particular, shade tolerance could be an advantageous trait for forest invaders, and previous research has shown that this trait is more prevalent among invasive shrubs than in invasive herbs (Martin et al., 2009). This is consistent with our results on trait selection across pathways: 74% of shrubs were introduced through gardening, while 75% of annual herbs and 37% of perennial herbs were introduced unintentionally. Thus, gardening plants could be more pre-adapted to tolerate shade in invaded forests, compared to unintentionally introduced plants. We note that this high prevalence of gardening plants in forests is consistent with previous work on forest edges in our study area: over 60% of non-native plants were introduced through gardening, and the presence of gardening plants was positively associated with the percentage of forest use in 1-km buffer around the sampled plots (González-Moreno et al., 2013).

Unintentionally introduced plants were the majority of invaders in meadows and scrublands. Since most unintentionally introduced plants were annuals (60%: 18 out of 30), they could be pre-adapted to taking advantage of anthropogenic disturbance in such habitats, thus becoming a majority of invaders. This is consistent with patterns in the prevailing growth form of non-native plants across the European continent: annuals were the prevailing growth form among grassland invaders (Axmanová et al., 2021), and the third most common growth form among scrubland invaders (Kalusová et al., 2023).

Unintentionally introduced plants were the sole invaders of rock outcrops, but it is uncertain about whether this pattern is consistent, as this habitat was represented by a single invaded plot. This contrasts to previous work on habitats along the coast in the metropolitan region of Barcelona: coastal rock outcrops were overwhelmingly invaded by intentionally introduced plants; 16 out of 18 non-native plants, in 16 patches (Başnou et al., 2015). The difference could be related to the sampling strategy: we sampled habitats based on a random distribution of points (inland rock outcrops were also sampled), while previous work (Başnou et al., 2015) sampled habitat patches located along the coast. Therefore, rock outcrops in our dataset were not overwhelmingly influenced by the invasion dynamics of coastal areas. In particular, rock outcrops in coastal areas could receive substantial propagule pressure from gardening plants. Indeed, we found gardening plants to be the majority of invaders in coastal habitats (54%, on average), possibly due to use of perennial succulents for xeriscaping (Sanz-Elorza et al., 2004a).

Appendix 3

Supplementary Material for Chapter 4

This Appendix contains

Supplementary Methods

Tables S3.1-S3.9

Figures S3.1-S3.9

Supplementary Results

Supplementary Discussion

Supplementary methods

Calculation of bioclimatic niche breadth. To calculate climatic niche breadth (in the native and invaded ranges), we calculated Principal Components Analysis on eight ecologically-meaningful variables that had |Pearson's r| < 0.75: BIO2 (Mean Diurnal Range), BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month, BIO8 (Mean Temperature of Wettest Quarter), BIO13 (Precipitation of Wettest Month), BIO17 (Precipitation of Driest Quarter), BIO18 (Precipitation of Warmest Quarter) and BIO19 (Precipitation of Coldest Quarter).

Details on the acquisition and processing of species occurrence and climatic data. We report methodological details following the relevant sections published guidelines (Feng et al., 2019).

(A) Occurrence data

A1) Source of occurrence data

GBiF (GBIF, 2022), via the 'rgbif' package (Chamberlain et al., 2022).

A2) Download date; version of data source

11 March 2022

A3) Basis of records

We removed fossil occurrences, plants in cultivation and absences.

A4) Spatial extent

Global excluding Europe.

A5) Temporal range

We did not perform filtering of occurrences based on year.

A6-1) Duplicate coordinates

We removed duplicate coordinates using the 'tidyverse' package (Wickham et al., 2019).

A6-2) Spatial and environmental outliers; error

We did not check potential outliers or errors, which would be unfeasible given the large sample size, and the lack of independent fine-scale distribution data for comparison. We think that we prevented some errors by excluding citizen-science datasets (iNaturalist, Pl@ntnet). Such datasets may be prone to including mistaken identifications, and records of plants cultivated in public or private gardens.

A6-3) Spatial coordinates and uncertainty

Our GBiF download excluded records without coordinates or with geospatial issues(GBIF, 2022). After the download, we removed coordinates located in country and province centroids, country capitals, and known biodiversity institutions (buffer of 2 km, using the 'CoordinateCleaner' package (Zizka et al., 2019). We also removed coordinates with: longitude = 0, latitude = 0, or located in the open sea, with the 'CoordinateCleaner' package (Zizka et al., 2019). We did not filter data based on coordinate uncertainty (such information was mostly absent).

A7-1) Sampling bias

We did not address sampling bias specifically, although the coordinate cleaning procedures reduced a pattern of overrepresentation of records in some areas.

A7-2) Spatial autocorrelation

We did not address the spatial distribution of the points. We did not address the spatial autocorrelation in bioclimatic variables extracted on those points either (Sillero & Barbosa, 2021).

(B) Environmental data

B1) Source

CHELSA v1.2 (Karger et al., 2017, 2018)

B2) Download date; version of data source

V1.2

B3) Spatial resolution

30 arc seconds = 0.5 arc minutes

B4) Temporal range

1979-2013

Supplementary tables

Table S3.1. Overview of the vegetation plot databases contributing to our final dataset. Number (N), proportional contribution (%) of plots used in our final dataset (N = 75,957). Databases are sorted in decreasing order according to proportional contribution. GIVD = Global Index of Vegetation-Plot Databases.

GIVD database name	GIVD code	N	%	Custodian	Deputy custodian
Czech National Phytosociological Database	EU-CZ-001	19,996	18	Milan Chytrý	Ilona Knollová
European Weed Vegetation Database	EU-00-028	12,314	11.1	Filip Küzmič	Urban Šilc
Dutch National Vegetation Database	EU-NL-001	10,428	9.4	Stephan Hennekens	Joop Schaminée
Polish Vegetation Database	EU-PL-001	10,027	9	Zygmunt Kącki	Grzegorz Swacha
SOPHY	EU-FR-003	7,097	6.4	Henry Brisse	Patrice de Ruffray
Vegetation Database of Slovenia	EU-SI-001	4,215	3.8	Urban Šilc	Filip Küzmič
Slovak Vegetation Database	EU-SK-001	4,061	3.6	Milan Valachovič	Jozef Šibík
Croatian Vegetation Database	EU-HR-002	3,981	3.6	Željko Škvorc	Daniel Krstonošić
Vegetation-Plot Database of the University of the Basque Country (BIOVEG)	EU-00-011	3,842	3.4	Idoia Biurrun	Itziar García-Mijangos
Austrian Vegetation Database	EU-AT-001	3,663	3.3	Wolfgang Willner	
Vegetation Plot Database - Sapienza University of Rome	EU-IT-011	3,577	3.2	Emiliano Agrillo	Fabio Attorre
Romanian Grassland Database	EU-RO-008	3,511	3.2	Eszter Ruprecht	Kiril Vassilev
INBOVEG 1	EU-BE-002	2,249	2	Els De Bie	
VegMV	EU-DE-001	1,653	1.5	Florian Jansen	Christian Berg
Forest Database of Southern Poland	EU-PL-003	1,564	1.4	Remigiusz Pielech	
Dutch Military Ranges Vegetation Database (DUMIRA)	EU-NL-003	1,373	1.2	Iris de Ronde	Rense Haveman
German Vegetation Reference Database (GVRD)	EU-DE-014	1,298	1.2	Ute Jandt	Helge Bruelheide
AMS-VegBank - Alma Mater Studiorum - University of Bologna	EU-IT-021	1,201	1.1	Alessandro Chiarucci	Vanessa Bruzzaniti
Balkan Vegetation Database	EU-00-019	1,155	1	Kiril Vassilev	Hristo Pedashenko

GIVD database name	GIVD code	N	%	Custodian	Deputy custodian
CoenoDat Hungarian Phytosociological Database	EU-HU-003	1,042	0.9	János Csiky	Zoltán Botta-Dukát
VegItaly	EU-IT-001	986	0.9	Roberto Venanzoni	Flavia Landucci
VegetWeb Germany 1	EU-DE-013	909	0.8	Florian Jansen	Jörg Ewald
UK National Vegetation Classification Database	EU-GB-001	874	0.8	John S. Rodwell	
German Grassland Vegetation Database (GrassVeg.DE)	EU-DE-020	843	0.8	Ricarda Pätsch	Jürgen Dengler
Swiss Forest Vegetation Database	EU-CH-005	654	0.6	Thomas Wohlgemuth	
Lithuanian vegetation Database	EU-LT-001	645	0.6	Valerius Rašomavičius	Domas Uogintas
Iberian and Macaronesian Vegetation Information System (SIVIM) – Floodplain Forests	EU-00-024	611	0.5	Idoia Biurrun	Xavier Font
European Boreal Forest Vegetation Database	EU-00-027	597	0.5	Anni Kanerva Jašková	
VegetWeb Germany 2	EU-DE-013	517	0.5	Friedemann Goral	Florian Jansen
KRITI	EU-GR-001	508	0.5	Erwin Bergmeier	
Mediterranean Ammophiletea database	EU-00-016	491	0.4	Corrado Marcenò	Borja Jiménez-Alfaro
Monitoring Effectiveness of Habitat Conservation in Switzerland	EU-CH-011	476	0.4	Ariel Bergamini	Steffen Boch
Irish Vegetation Database	EU-IE-001	471	0.4	Úna FitzPatrick	Lynda Weekes
Romanian Forest Database	EU-RO-007	433	0.4	Adrian Indreica	Pavel Dan Turtureanu
Iberian and Macaronesian Vegetation Information System (SIVIM) - Catalonia	EU-00-004	376	0.3	Xavier Font	
Iberian and Macaronesian Vegetation Information System (SIVIM) - Grasslands	EU-00-004	360	0.3	Maria Pilar Rodríguez-Rojo	Xavier Font
Gravel bar vegetation database	EU-00-025	356	0.3	Veronika Kalníková	Helmut Kudrnovsky
Vegetation database of Habitats in the Italian Alps - HabItAlp - HabitAlp	EU-IT-010	340	0.3	Laura Casella	Pierangela Angelini
Masaryk University's Gap-Filling Database of European Vegetation	EU-00-031	308	0.3	Milan Chytrý	Ilona Knollová

GIVD database name	GIVD code	N	%	Custodian	Deputy custodian
Hellenic Natura 2000 Vegetation Database (HelNatVeg)	EU-GR-005	257	0.2	Panayotis Dimopoulos	Ioannis Tsiripidis
Balkan Dry Grasslands Database	EU-00-013	231	0.2	Kiril Vassilev	Armin Macanović
RanVegDunes	EU-IT-020	176	0.2	Alicia Acosta	
Semi-natural Grassland Vegetation Database of Latvia	EU-LV-001	175	0.2	Solvita Rūsiņa	
Vegetation Database Grassland Vegetation of Serbia	EU-RS-002	167	0.1	Svetlana Aćić	Zora Dajić Stevanović
CircumMed Pine Forest database	EU-00-026	145	0.1	Gianmaria Bonari	
The Nordic Vegetation Database	EU-00-018	144	0.1	Jonathan Lenoir	Jens-Christian Svenning
SE Europe forest database	EU-00-021	129	0.1	Andraž Čarni	
INBOVEG 2	EU-BE-002	126	0.1	Els De Bie	
Nordic-Baltic Grassland Vegetation Database (NBGVD)	EU-00-002	123	0.1	Jürgen Dengler	Łukasz Kozub
Coastal Vegetation Germany	EU-DE-035	101	0.1	Maike Isermann	Florian Jansen
VegetWeb Germany 3	EU-DE-013	98	0.1	Friedemann Goral	Florian Jansen
European Coastal Vegetation Database	EU-00-017	94	0.1	John Janssen	
Iberian and Macaronesian Vegetation Information System (SIVIM) - Sclerophyllous, pinus	EU-00-004	93	0.1	Federico Fernández-González	Xavier Font
Iberian and Macaronesian Vegetation Information System (SIVIM) – Deciduous Forests	EU-00-023	46	< 0.1	Juan Antonio Campos	Xavier Font
Bulgarian Vegetation Database	EU-BG-001	44	< 0.1	Iva Apostolova	Desislava Sopotlieva
VEGFRANCE	EU-FR-004	44	< 0.1	Jan-Bernard Bouzillé	Pauline Delbosc
Iberian and Macaronesian Vegetation Information System (SIVIM)	EU-00-004	28	< 0.1	Xavier Font	
Database Schleswig-Holstein (Northern Germany)	EU-DE-040	27	< 0.1	Joachim Schrautzer	
Iberian and Macaronesian Vegetation Information System (SIVIM) - Sclerophyllous	EU-00-004	26	< 0.1	Federico Fernández-González	Xavier Font
Vegetation Database of the Republic of Macedonia	EU-MK-001	21	< 0.1	Renata Ćušterevska	

GIVD database name	GIVD code	N	%	Custodian	Deputy custodian
Database of Forest Vegetation in Republic of Serbia + Vegetation Database of Northern Part of Serbia (AP Vojvodina)	EU-RS-003 + EU-RS-004	14	< 0.1	Mirjana Krstivojević Ćuk	
Vegetation database of Habitats in the Italian Alps - HabItAlp - Mires	EU-IT-010	13	< 0.1	Laura Casella	Marco Massimi
European Mire Vegetation Database	EU-00-022	12	< 0.1	Tomáš Peterka	Martin Jiroušek
Beech Forest Vegetation Database of SE Balkan	EU-00-012	11	< 0.1	Aleksander Marinšek	
Iberian and Macaronesian Vegetation Information System (SIVIM) - Scrubs	EU-00-004	10	< 0.1	Rosario G Gavilán	Xavier Font
Vegetation Database of Albania	EU-AL-001	9	< 0.1	Michele De Sanctis	Giuliano Fanelli
Serra da Estrela database	EU-PT-001	9	< 0.1	Jan Jansen	
FloodplainMeadows	EU-GB-004	2	< 0.1	Irina Tatarenko	
Vegetation Database of Ukraine and Adjacent Parts of Russia	EU-UA-006	2	< 0.1	Viktor Onyshchenko	Vitaliy Kolomiychuk
Iberian and Macaronesian Vegetation Information System (SIVIM) - Alpine	EU-00-004	1	< 0.1	Borja Jiménez-Alfaro	Xavier Font

Table S3.2. Overview of all the full models of niche breadth: five metrics of niche breadth x three ways to code introduction pathways, yielding a total of 15 models. We present relevant summaries of the full models, which were fitted prior to the multimodel inference procedure. Sample size (N) varies across models because models in which pathways were coded through two non-exclusive categories contain 62 duplicated neophytes, and because biotic niche breadth was not available for five neophytes (for such species, there were less than ten plots after plots with outlying species composition were removed). R^2_{adj} and Pagel's lambda were obtained with the 'phylolm' package (Tung Ho & Ané, 2014). Variance inflation factors (VIFs) were calculated with the performance package (Lüdecke et al., 2021). A likelihood-ratio test compared the full model to an intercept-only model: significant p-values indicate significant full models. Abbreviations: Intent.= Intentional, LRT = Likelihood Ratio Test, lv. = level of the EUNIS hierarchical habitat classification, nb = niche breadth, p-v = p-value, Unint. = Unintentional, VIF = Variance Inflation Factor

Niche breadth metric	Introduction pathway coding	N	R^2_{adj}	Pagel's λ	Highest VIF	LRT (p-v)
Habitat range (lv. 1)	Intent. + Unint. vs. Intent. vs. Unint.	220	0.250	0.000	2.915	0.000
Habitat range (lv. 1)	Intent. vs. Unint., non-exclusive	282	0.261	0.000	2.467	0.000
Habitat range (lv. 1)	Intentionality proportion	220	0.234	0.000	2.896	0.000
Habitat range (lv. 2)	Intent. + Unint. vs. Intent. vs. Unint.	220	0.297	0.000	2.915	0.000
Habitat range (lv. 2)	Intent. vs. Unint., non-exclusive	282	0.299	0.000	2.467	0.000
Habitat range (lv. 2)	Intentionality proportion	220	0.278	0.000	2.896	0.000
Habitat range (lv. 3)	Intent. + Unint. vs. Intent. vs. Unint.	220	0.343	0.000	2.947	0.000
Habitat range (lv. 3)	Intent. vs. Unint., non-exclusive	282	0.338	0.000	2.467	0.000
Habitat range (lv. 3)	Intentionality proportion	220	0.323	0.000	2.931	0.000
Biotic nb	Intent. + Unint. vs. Intent. vs. Unint.	215	0.058	0.507	2.028	0.012
Biotic nb	Intent. vs. Unint., non-exclusive	277	0.065	0.764	1.620	0.002
Biotic nb	Intentionality proportion	215	0.059	0.506	2.057	0.011
Climatic nb	Intent. + Unint. vs. Intent. vs. Unint.	220	0.131	0.299	2.183	0.000
Climatic nb	Intent. vs. Unint., non-exclusive	282	0.129	0.514	1.755	0.000
Climatic nb	Intentionality proportion	220	0.131	0.298	2.193	0.000

Table S3.3. Model-averaged coefficients (95% confidence interval) of drivers of niche breadth across of non-native plants across Europe. This table shows the results for 15 phylogenetic least square models: five metrics of niche breadth x three ways to code introduction pathways. a) pathways coded as three categories (Intentional vs Unintentional vs Both), which are plotted in Fig. 4.1 (Figs. S3.2-3.4 include habitat range at levels 2-3); b-c) pathways coded as two categories (Intentional vs Unintentional) and as intentionality proportion, which are plotted in Figs. S3.2-3.4.

(a) Pathways coded as three categories (Intentional vs Unintentional vs Both)

Explanatory variables	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Intercept	1.559 (1.302, 1.816)	2.208 (1.92, 2.497)	3.019 (2.674, 3.364)	5.346 (4.288, 6.404)	0.786 (0.528, 1.043)
Introduction pathway: Intentional (only)	-0.164 (-0.347, 0.019)	-0.386 (-0.621, -0.151)	-0.497 (-0.774, -0.221)	-0.045 (-0.285, 0.196)	-0.061 (-0.192, 0.07)
Introduction pathway: Unintentional (only)	-0.294 (-0.493, -0.095)	-0.415 (-0.662, -0.167)	-0.459 (-0.75, -0.169)	-0.063 (-0.35, 0.223)	-0.038 (-0.14, 0.064)
Minimum residence time (linear term)	0.203 (0.135, 0.27)	0.276 (0.189, 0.363)	0.465 (0.334, 0.597)	0.204 (0.07, 0.339)	0.016 (-0.025, 0.057)
Minimum residence time (quadratic term)			-0.082 (-0.162, -0.002)		
Native climatic niche breadth	0.039 (-0.041, 0.119)	0.061 (-0.047, 0.169)	0.046 (-0.068, 0.161)	0.164 (-0.001, 0.329)	0.099 (0.059, 0.14)
Height	-0.013 (-0.072, 0.046)	0.001 (-0.052, 0.053)	0.03 (-0.075, 0.136)	0.064 (-0.13, 0.258)	0.049 (-0.02, 0.118)
Dispersal syndrome: Endozoochorous	-0.059 (-0.248, 0.13)	-0.036 (-0.296, 0.225)	0.033 (-0.262, 0.328)	-0.005 (-0.115, 0.106)	0.035 (-0.095, 0.165)
Dispersal syndrome: Epizoochorous	-0.068 (-0.327, 0.19)	-0.287 (-0.686, 0.111)	-0.284 (-0.766, 0.199)	-0.008 (-0.145, 0.13)	0.029 (-0.097, 0.156)
Dispersal syndrome: Unspecific	-0.145 (-0.399, 0.11)	-0.302 (-0.567, -0.038)	-0.254 (-0.588, 0.079)	-0.009 (-0.126, 0.108)	0.035 (-0.089, 0.159)

Explanatory variables	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Growth form: Perennial herbaceous	-0.029 (-0.154, 0.096)	-0.028 (-0.172, 0.115)	-0.021 (-0.161, 0.118)	0.017 (-0.139, 0.174)	-0.004 (-0.041, 0.034)
Growth form: Shrub/Tree	-0.052 (-0.258, 0.155)	-0.053 (-0.289, 0.184)	-0.056 (-0.332, 0.22)	0.047 (-0.227, 0.32)	-0.003 (-0.052, 0.046)

(b) Pathways coded as two categories (Intentional vs Unintentional) and as intentionality proportion

Explanatory variables	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Intercept	1.554 (1.209, 1.898)	2.202 (1.929, 2.476)	2.887 (2.192, 3.582)	5.288 (3.753, 6.823)	0.769 (0.466, 1.072)
Introduction pathway: Unintentional (non-exclusive)	-0.018 (-0.105, 0.069)	-0.002 (-0.088, 0.084)	0.004 (-0.098, 0.107)	-0.005 (-0.117, 0.108)	0.002 (-0.03, 0.035)
Minimum residence time (linear term)	0.293 (0.222, 0.364)	0.414 (0.32, 0.509)	0.575 (0.46, 0.689)	0.22 (0.109, 0.331)	0.033 (-0.005, 0.071)
Minimum residence time (quadratic term)	-0.057 (-0.105, -0.009)	-0.079 (-0.143, -0.014)	-0.118 (-0.198, -0.039)		
Native climatic niche breadth	0.049 (-0.028, 0.127)	0.085 (-0.017, 0.186)	0.091 (-0.047, 0.229)	0.169 (0.041, 0.296)	0.102 (0.069, 0.135)
Height	-0.015 (-0.073, 0.043)	-0.003 (-0.055, 0.049)	0.036 (-0.081, 0.152)	0.045 (-0.118, 0.208)	0.034 (-0.025, 0.092)
Dispersal syndrome: Endozoochorous	-0.044 (-0.225, 0.137)	-0.051 (-0.298, 0.196)	0.004 (-0.302, 0.31)	0.005 (-0.107, 0.117)	0.017 (-0.074, 0.109)
Dispersal syndrome: Epizoochorous	-0.21 (-0.527, 0.106)	-0.514 (-0.904, -0.125)	-0.55 (-1.084, -0.016)	-0.004 (-0.114, 0.106)	0.012 (-0.067, 0.09)
Dispersal syndrome: Unspecific	-0.169 (-0.384, 0.046)	-0.304 (-0.523, -0.085)	-0.302 (-0.614, 0.011)	-0.004 (-0.088, 0.081)	0.016 (-0.065, 0.096)

Explanatory variables	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Growth form: Perennial herbaceous	-0.052 (-0.187, 0.083)	-0.096 (-0.279, 0.087)	-0.089 (-0.299, 0.121)	0.047 (-0.165, 0.258)	-0.002 (-0.031, 0.026)
Growth form: Shrub/Tree	-0.115 (-0.373, 0.142)	-0.265 (-0.61, 0.08)	-0.307 (-0.782, 0.168)	0.102 (-0.27, 0.474)	-0.002 (-0.038, 0.034)

(c) Pathways coded as intentionality proportion

Explanatory variables	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Intercept	1.511 (1.195, 1.826)	2.221 (1.898, 2.545)	2.999 (2.588, 3.41)	5.376 (4.301, 6.45)	0.788 (0.526, 1.049)
Introduction pathway (Intentionality proportion, linear term)	-0.031 (-0.128, 0.065)	-0.17 (-0.315, -0.026)	-0.2 (-0.385, -0.014)	-0.015 (-0.144, 0.114)	-0.033 (-0.107, 0.041)
Introduction pathway (Intentionality proportion, quadratic term)	-0.11 (-0.305, 0.086)	-0.285 (-0.491, -0.079)	-0.31 (-0.574, -0.046)	-0.067 (-0.324, 0.19)	-0.04 (-0.136, 0.056)
Minimum residence time (linear term)	0.225 (0.158, 0.293)	0.306 (0.22, 0.392)	0.504 (0.373, 0.635)	0.204 (0.071, 0.337)	0.019 (-0.023, 0.061)
Minimum residence time (quadratic term)			-0.082 (-0.164, -0.001)		
Native climatic niche breadth	0.042 (-0.04, 0.123)	0.058 (-0.05, 0.167)	0.05 (-0.069, 0.169)	0.165 (0, 0.33)	0.099 (0.059, 0.14)
Height	-0.014 (-0.075, 0.047)	0 (-0.051, 0.051)	0.027 (-0.076, 0.129)	0.064 (-0.13, 0.257)	0.05 (-0.019, 0.119)
Dispersal syndrome: Endozoochorous	-0.057 (-0.245, 0.132)	-0.038 (-0.306, 0.229)	0.029 (-0.274, 0.331)	-0.004 (-0.11, 0.102)	0.034 (-0.095, 0.162)
Dispersal syndrome: Epizoochorous	-0.092 (-0.367, 0.183)	-0.352 (-0.752, 0.048)	-0.339 (-0.849, 0.17)	-0.007 (-0.139, 0.125)	0.027 (-0.095, 0.15)

Explanatory variables	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Dispersal syndrome: Unspecific	-0.135 (-0.392, 0.123)	-0.322 (-0.572, -0.072)	-0.27 (-0.609, 0.069)	-0.008 (-0.12, 0.104)	0.034 (-0.088, 0.155)
Growth form: Perennial herbaceous	-0.024 (-0.141, 0.093)	-0.025 (-0.163, 0.113)	-0.024 (-0.176, 0.127)	0.015 (-0.136, 0.165)	-0.003 (-0.04, 0.034)
Growth form: Shrub/Tree	-0.043 (-0.233, 0.146)	-0.049 (-0.277, 0.18)	-0.071 (-0.381, 0.238)	0.041 (-0.216, 0.299)	-0.003 (-0.052, 0.045)

Table S3.4. Relative importance of drivers of niche breadth for non-native plants in Europe, approximated through standardized general dominance: proportional contribution to the total R^2_{adj} of the PGLS model. Note that dispersal syndrome and growth form yielded substantially negative values of relative importance in models of biotic niche breadth, so values from models without these variables are provided inside the parentheses. Abbreviations: Intent. = Intentional, Unint. = Unintentional

Introduction pathway coding	Variable	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
Intent. + Unint. vs. Intent. vs. Unint.	Introduction pathway (Intent. + Unint. vs. Intent. vs. Unint.)	0.257	0.286	0.258	0.209 (0.16)	0.163
	Growth form	-0.008	-0.005	-0.003	-0.098 (-)	0.026
	Dispersal syndrome	0.083	0.103	0.065	-0.135 (-)	0.022
	Native climatic niche breadth	0.039	0.053	0.031	0.434 (0.334)	0.663
	Minimum residence time (quadratic for habitat range level 3)	0.635	0.572	0.644	0.593 (0.472)	0.06
	Height	-0.006	-0.009	0.006	-0.003 (0.034)	0.066
Intent. vs. Unint., non-exclusive	Introduction pathway (Intentional vs. Unintentional, non-exclusive)	-0.001	-0.007	-0.007	-0.052 (-0.044)	-0.018
	Growth form	0.026	0.03	0.031	-0.032 (-)	-0.004
	Dispersal syndrome	0.086	0.116	0.085	-0.119 (-)	-0.004
	Native climatic niche breadth	0.052	0.081	0.053	0.42 (0.352)	0.868
	Minimum residence time (quadratic for habitat range levels 1-3)	0.832	0.783	0.833	0.795 (0.686)	0.125
	Height	0.004	-0.003	0.005	-0.013 (0.006)	0.032
Intentionality proportion	Introduction pathway (Intentionality proportion, includes a quadratic term)	0.14	0.164	0.137	0.191 (0.158)	0.146
	Growth form	-0.007	-0.006	-0.002	-0.111 (-)	0.025
	Dispersal syndrome	0.088	0.115	0.072	-0.133 (-)	0.019

Introduction pathway coding	Variable	Habitat range (level 1)	Habitat range (level 2)	Habitat range (level 3)	Biotic niche breadth	Climatic niche breadth
	Native climatic niche breadth	0.043	0.058	0.034	0.438 (0.335)	0.667
	Minimum residence time (quadratic for habitat range level 3)	0.742	0.679	0.755	0.62 (0.48)	0.074
	Height	-0.006	-0.01	0.005	-0.005 (0.027)	0.069

Table S3.5. Habitat harshness at level 3 of EUNIS hierarchical habitat classification. Based on expert knowledge, each habitat was classified into three, non-exclusive harshness categories: drought, salinity and oligotrophy (N = 166 invaded habitsts with sufficient detail to be classified to level 3). Abbreviations: EUNIS = European Nature Information System, MA = littoral biogenic (marine habitats), N = coastal habitats, Q = wetlands, R = grasslands, S = heathlands, scrub and tundra, T = forests, U = little soil, sparse vegetation, V = man-made.

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
MA221	Atlantic saltmarsh driftline	0	1	0
MA222	Atlantic upper saltmarsh	0	1	0
MA223	Atlantic upper-mid saltmarsh and saline and brackish reed, rush and sedge bed	0	1	0
MA224	Atlantic mid-low saltmarsh	0	1	0
MA225	Atlantic pioneer saltmarsh	0	1	0
MA232	Baltic coastal meadow	0	1	0
MA241	Black Sea littoral saltmarsh	0	1	0
MA251	Mediterranean upper saltmarsh	0	1	0
MA252	Mediterranean upper-mid saltmarsh and saline and brackish reed, rush and sedge bed	0	1	0
MA253	Mediterranean mid-low saltmarsh	0	1	0
N11	Atlantic, Baltic and Arctic sand beach	0	1	1
N12	Mediterranean and Black Sea sand beach	0	1	1
N13	Atlantic and Baltic shifting coastal dune	1	0	1
N14	Mediterranean, Macaronesian and Black Sea shifting coastal dune	1	0	1
N15	Atlantic and Baltic coastal dune grassland (grey dune)	1	0	1
N16	Mediterranean and Macaronesian coastal dune grassland (grey dune)	1	0	1
N17	Black Sea coastal dune grassland (grey dune)	1	0	1
N18	Atlantic and Baltic coastal *Empetrum* heath	1	0	1
N19	Atlantic coastal *Calluna* and *Ulex* heath	0	0	1

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
N1A	Atlantic and Baltic coastal dune scrub	0	0	0
N1B	Mediterranean and Black Sea coastal dune scrub	1	0	0
N1D	Atlantic and Baltic broad-leaved coastal dune forest	0	0	0
N1F	Baltic coniferous coastal dune forest	0	0	0
N1G	Mediterranean coniferous coastal dune forest	1	0	0
N1H	Atlantic and Baltic moist and wet dune slack	0	0	1
N1J	Mediterranean and Black Sea moist and wet dune slack	0	0	1
N21	Atlantic, Baltic and Arctic coastal shingle beach	0	1	0
N22	Mediterranean and Black Sea coastal shingle beach	0	1	0
N31	Atlantic and Baltic rocky sea cliff and shore	1	1	1
N32	Mediterranean and Black Sea rocky sea cliff and shore	1	1	1
N35	Mediterranean and Black Sea soft sea cliff	1	1	1
Q11	Raised bog	0	0	1
Q12	Blanket bog	0	0	1
Q21	Oceanic valley mire	0	0	1
Q22	Poor fen	0	0	1
Q24	Intermediate fen and soft-water spring mire	0	0	1
Q25	Non-calcareous quaking mire	0	0	1
Q41	Alkaline, calcareous, carbonate-rich small-sedge spring fen	0	0	1
Q42	Extremely rich moss-sedge fen	0	0	1
Q43	Tall-sedge base-rich fen	0	0	1
Q51	Tall-helophyte bed	0	0	0

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
Q52	Small-helophyte bed	0	0	0
Q53	Tall-sedge bed	0	0	0
Q54	Inland saline or brackish helophyte bed	0	1	0
R11	Pannonian and Pontic sandy steppe	1	0	1
R12	Cryptogam- and annual-dominated vegetation on siliceous rock outcrops	1	0	1
R13	Cryptogam- and annual-dominated vegetation on calcareous and ultramafic rock outcrops	1	0	1
R16	Perennial rocky grassland of Central and South-Eastern Europe	1	0	1
R17	Heavy-metal dry grassland of the Balkans	1	0	1
R18	Perennial rocky calcareous grassland of subatlantic-submediterranean Europe	1	0	1
R1A	Semi-dry perennial calcareous grassland (meadow steppe)	1	0	1
R1B	Continental dry grassland (true steppe)	1	0	1
R1D	Mediterranean closely grazed dry grassland	1	0	1
R1E	Mediterranean tall perennial dry grassland	1	0	1
R1F	Mediterranean annual-rich dry grassland	1	0	1
R1M	Lowland to montane, dry to mesic grassland usually dominated by *Nardus stricta*	0	0	1
R1P	Oceanic to subcontinental inland sand grassland on dry acid and neutral soils	1	0	1
R1Q	Inland sanddrift and dune with siliceous grassland	1	0	1
R1R	Mediterranean to Atlantic open, dry, acid and neutral grassland	1	0	1
R21	Mesic permanent pasture of lowlands and mountains	0	0	0
R22	Low and medium altitude hay meadow	0	0	0

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
R23	Mountain hay meadow	0	0	0
R24	Iberian summer pasture (vallicar)	1	0	1
R31	Mediterranean tall humid inland grassland	0	0	0
R33	Mediterranean short moist grassland of mountains	0	0	0
R34	Submediterranean moist meadow	0	0	0
R35	Moist or wet mesotrophic to eutrophic hay meadow	0	0	0
R36	Moist or wet mesotrophic to eutrophic pasture	0	0	0
R37	Temperate and boreal moist or wet oligotrophic grassland	0	0	1
R43	Temperate acidophilous alpine grassland	0	0	1
R51	Thermophilous forest fringe of base-rich soils	0	0	1
R52	Forest fringe of acidic nutrient-poor soils	0	0	1
R54	*Pteridium aquilinum* vegetation	0	0	1
R55	Lowland moist or wet tall-herb and fern fringe	0	0	0
R56	Montane to subalpine moist or wet tall-herb and fern fringe	0	0	0
R57	Herbaceous forest clearing vegetation	0	0	0
R61	Mediterranean inland salt steppe	1	1	0
R62	Continental inland salt steppe	1	1	0
R63	Temperate inland salt marsh	0	1	0
S21	Subarctic and alpine dwarf *Salix* scrub	0	0	1
S22	Alpine and subalpine ericoid heath	0	0	1
S23	Alpine and subalpine *Juniperus* scrub	0	0	1
S25	Subalpine and subarctic deciduous scrub	0	0	0
S31	Lowland to montane temperate and submediterranean *Juniperus* scrub	0	0	0

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
S32	Temperate *Rubus* scrub	0	0	0
S33	Lowland to montane temperate and submediterranean genistoid scrub	0	0	1
S34	Balkan-Anatolian submontane genistoid scrub	1	0	0
S35	Temperate and submediterranean thorn scrub	0	0	0
S36	Low steppic scrub	1	0	0
S37	*Corylus avellana* scrub	0	0	0
S38	Temperate forest clearing scrub	0	0	0
S41	Wet heath	0	0	1
S42	Dry heath	0	0	1
S51	Mediterranean maquis and arborescent matorral	1	0	0
S52	Submediterranean pseudomaquis	1	0	0
S53	*Spartium junceum* scrub	1	0	0
S54	Thermomediterranean arid scrub	1	0	0
S61	Western basiphilous garrigue	1	0	0
S62	Western acidophilous garrigue	1	0	0
S63	Eastern garrigue	1	0	0
S65	Mediterranean gypsum scrub	1	1	0
S66	Mediterranean halo-nitrophilous scrub	1	1	0
S91	Temperate riparian scrub	0	0	0
S92	*Salix* fen scrub	0	0	1
S93	Mediterranean riparian scrub	0	0	0
T11	Temperate *Salix* and *Populus* riparian forest	0	0	0
T12	*Alnus glutinosa-Alnus incana* forest on riparian and mineral soils	0	0	0
T13	Temperate hardwood riparian forest	0	0	0

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
T14	Mediterranean and Macaronesian riparian forest	0	0	0
T15	Broadleaved swamp forest on non-acid peat	0	0	0
T16	Broadleaved mire forest on acid peat	0	0	1
T17	*Fagus* forest on non-acid soils	0	0	0
T18	*Fagus* forest on acid soils	0	0	1
T19	Temperate and submediterranean thermophilous deciduous forest	1	0	0
T1A	Mediterranean thermophilous deciduous forest	1	0	0
T1B	Acidophilous *Quercus* forest	0	0	1
T1D	Southern European mountain *Betula* and *Populus tremula* forest on mineral soils	0	0	0
T1E	*Carpinus* and *Quercus* mesic deciduous forest	0	0	0
T1F	Ravine forest	0	0	0
T1G	*Alnus cordata* forest	0	0	0
T1H	Broadleaved deciduous plantation of non site-native trees	0	0	0
T21	Mediterranean evergreen *Quercus* forest	1	0	0
T22	Mainland laurophyllous forest	0	0	0
T24	*Olea europaea-Ceratonia siliqua* forest	1	0	0
T25	*Phoenix theophrasti* vegetation	0	0	0
T27	*Ilex aquifolium* forest	0	0	0
T29	Broadleaved evergreen plantation of non site-native trees	0	0	0
T31	Temperate mountain *Picea* forest	0	0	0
T32	Temperate mountain *Abies* forest	0	0	0
T33	Mediterranean mountain *Abies* forest	1	0	0

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
T34	Temperate subalpine *Larix*, *Pinus cembra* and *Pinus uncinata* forest	0	0	0
T35	Temperate continental *Pinus sylvestris* forest	0	0	1
T36	Temperate and submediterranean montane *Pinus sylvestris-Pinus nigra* forest	1	0	1
T37	Mediterranean montane *Pinus sylvestris-Pinus nigra* forest	1	0	1
T3A	Mediterranean lowland to submontane *Pinus* forest	1	0	1
T3C	*Taxus baccata* forest	0	0	0
T3D	Mediterranean Cupressaceae forest	1	0	1
T3F	Dark taiga	0	0	0
T3G	*Pinus sylvestris* light taiga	0	0	0
T3J	*Pinus* and *Larix* mire forest	0	0	1
T3K	Picea mire forest	0	0	1
T3M	Coniferous plantation of non site-native trees	0	0	0
U22	Temperate high-mountain siliceous scree	1	0	1
U23	Temperate, lowland to montane siliceous scree	1	0	1
U24	Mediterranean siliceous scree	1	0	1
U26	Temperate high-mountain base-rich scree and moraine	1	0	1
U27	Temperate, lowland to montane base-rich scree	1	0	1
U28	Western Mediterranean base-rich scree	1	0	1
U33	Temperate, lowland to montane siliceous inland cliff	1	0	1
U34	Mediterranean siliceous inland cliff	1	0	1
U37	Temperate, lowland to montane base-rich inland cliff	1	0	1

EUNIS 2020 code	EUNIS 2020 habitat name	Drought	Salinity	Oligotrophy
U38	Mediterranean base-rich inland cliff	1	0	1
U3A	Temperate ultramafic inland cliff	1	0	1
U3D	Wet inland cliff	0	0	1
V11	Intensive unmixed crops	0	0	0
V12	Mixed crops of market gardens and horticulture	0	0	0
V13	Arable land with unmixed crops grown by low-intensity agricultural methods	0	0	0
V14	Inundated or inundatable cropland, including rice fields	0	0	0
V15	Bare tilled, fallow or recently abandoned arable land	0	0	0
V32	Mediterranean subnitrophilous annual grasslands	1	0	0
V33	Dry mediterranean lands with unpalatable non-vernal herbaceous vegetation	1	0	0
V34	Trampled xeric grassland with annuals	1	0	0
V35	Trampled mesophilous grassland with annuals	0	0	0
V37	Annual anthropogenic herbaceous vegetation	0	0	0
V38	Dry perennial anthropogenic herbaceous vegetation	1	0	0
V39	Mesic perennial anthropogenic herbaceous vegetation	0	0	0

Table S3.6. Distribution of non-native plants across, (**a**) harsh environmental conditions, and (**b**) habitats. Table shows the number (N) and percentage (%) of invaded plots per given harsh condition or habitat. Species are sorted alphabetically, and those with the top ten highest number of invaded plots per harsh condition or habitat are in bold. Abbreviations: Pint = intentionality proportion.

(a) Harsh environmental conditions

Species name		Salinity		Oligotrophy		Drought	
	Pint	N	%	N	%	N	%
Abies grandis	1.000	0	0.00	0	0.00	0	0.00
Acacia dealbata	1.000	0	0.00	9	0.11	27	0.26
Acacia saligna	1.000	0	0.00	32	0.40	45	0.44
Acaena novae-zelandiae	0.000	0	0.00	5	0.06	5	0.05
Acalypha virginica	0.333	0	0.00	3	0.04	0	0.00
Acer negundo	0.909	0	0.00	22	0.28	58	0.57
Acorus calamus	0.889	0	0.00	14	0.18	0	0.00
Agave americana	1.000	2	0.27	20	0.25	40	0.39
Ageratina adenophora	0.500	0	0.00	0	0.00	1	0.01
Ailanthus altissima	1.000	2	0.27	27	0.34	100	0.98
Alternanthera caracasana	0.000	0	0.00	0	0.00	11	0.11
Amaranthus albus	0.222	2	0.27	8	0.10	185	1.81
Amaranthus blitoides	0.000	2	0.27	2	0.03	148	1.45
Amaranthus cruentus	1.000	0	0.00	0	0.00	13	0.13
Amaranthus deflexus	0.000	3	0.41	4	0.05	134	1.31
Amaranthus hybridus	0.143	0	0.00	2	0.03	70	0.68
Amaranthus hypochondriacus	1.000	0	0.00	1	0.01	2	0.02
Amaranthus muricatus	0.000	2	0.27	2	0.03	32	0.31
Amaranthus powellii	0.000	0	0.00	2	0.03	28	0.27
Amaranthus retroflexus	0.091	5	0.68	**29**	**0.36**	573	5.60
Amaranthus viridis	0.000	1	0.14	1	0.01	38	0.37
Ambrosia artemisiifolia	0.000	1	0.14	46	0.58	164	1.60
Ambrosia psilostachya	0.000	7	0.95	77	0.96	104	1.02
Amorpha fruticosa	1.000	3	0.41	22	0.28	39	0.38
Apios americana	1.000	0	0.00	0	0.00	0	0.00
Arctotheca calendula	0.500	0	0.00	8	0.10	66	0.65
Aronia x prunifolia	1.000	0	0.00	34	0.43	0	0.00
Artemisia biennis	0.000	0	0.00	0	0.00	2	0.02
Artemisia verlotiorum	0.286	0	0.00	2	0.03	95	0.93

Species name	Pint	Salinity		Oligotrophy		Drought	
		N	%	N	%	N	%
Asclepias syriaca	1.000	0	0.00	5	0.06	26	0.25
Baccharis halimifolia	1.000	**52**	**7.06**	18	0.23	5	0.05
Bidens aureus	0.000	0	0.00	0	0.00	12	0.12
Bidens bipinnatus	0.333	0	0.00	0	0.00	4	0.04
Bidens connatus	0.000	0	0.00	6	0.08	1	0.01
Bidens frondosus	0.182	4	0.54	40	0.50	51	0.50
Bidens subalternans	0.000	0	0.00	0	0.00	4	0.04
Bidens vulgatus	0.000	0	0.00	0	0.00	0	0.00
Buddleja davidii	1.000	1	0.14	5	0.06	13	0.13
Caragana arborescens	1.000	0	0.00	1	0.01	0	0.00
Carpobrotus acinaciformis	1.000	**14**	**1.90**	66	0.83	93	0.91
Carpobrotus edulis	1.000	**22**	**2.99**	121	1.51	142	1.39
Cedrus atlantica	1.000	0	0.00	12	0.15	32	0.31
Celtis occidentalis	1.000	0	0.00	0	0.00	4	0.04
Cenchrus longisetus	1.000	0	0.00	4	0.05	8	0.08
Cenchrus longispinus	0.000	0	0.00	10	0.13	10	0.10
Cenchrus spinifex	0.000	4	0.54	32	0.40	34	0.33
Ceratochloa carinata	0.600	0	0.00	0	0.00	12	0.12
Ceratochloa cathartica	0.333	0	0.00	1	0.01	48	0.47
Chamaecyparis lawsoniana	1.000	0	0.00	2	0.03	0	0.00
Claytonia perfoliata	0.571	0	0.00	13	0.16	18	0.18
Claytonia sibirica	1.000	0	0.00	2	0.03	0	0.00
Collomia grandiflora	1.000	0	0.00	10	0.13	16	0.16
Cornus sericea	1.000	0	0.00	2	0.03	7	0.07
Cortaderia selloana	1.000	9	1.22	4	0.05	12	0.12
Cotoneaster horizontalis	1.000	0	0.00	3	0.04	1	0.01
Cotoneaster lucidus	1.000	0	0.00	11	0.14	0	0.00
Cotula australis	0.000	0	0.00	0	0.00	10	0.10
Cotula coronopifolia	0.222	**46**	**6.24**	5	0.06	10	0.10
Crassula lycopodioides	1.000	0	0.00	**189**	**2.37**	198	1.94
Cuscuta campestris	0.000	2	0.27	19	0.24	40	0.39
Cyperus eragrostis	0.000	1	0.14	1	0.01	14	0.14
Datura stramonium	0.667	4	0.54	5	0.06	98	0.96

Species name	Pint	Salinity		Oligotrophy		Drought	
		N	%	N	%	N	%
Deutzia scabra	1.000	0	0.00	0	0.00	0	0.00
Dichondra micrantha	1.000	0	0.00	0	0.00	10	0.10
Dysphania ambrosioides	0.700	6	0.81	9	0.11	81	0.79
Dysphania multifida	0.000	0	0.00	0	0.00	13	0.13
Dysphania pumilio	0.000	0	0.00	0	0.00	7	0.07
Echinochloa oryzoides	0.000	0	0.00	0	0.00	2	0.02
Echinocystis lobata	1.000	0	0.00	5	0.06	8	0.08
Elaeagnus pungens	1.000	0	0.00	1	0.01	0	0.00
Eleusine tristachya	0.000	0	0.00	2	0.03	11	0.11
Epilobium brachycarpum	0.000	0	0.00	4	0.05	16	0.16
Epilobium brunnescens	0.500	0	0.00	13	0.16	0	0.00
Epilobium ciliatum	0.000	2	0.27	57	0.71	147	1.44
Eragrostis pectinacea	0.000	0	0.00	0	0.00	1	0.01
Eragrostis virescens	0.000	0	0.00	0	0.00	2	0.02
Erechtites hieraciifolius	0.000	0	0.00	15	0.19	9	0.09
Erigeron annuus	0.364	0	0.00	**454**	**5.68**	1,049	10.26
Erigeron bonariensis	0.000	12	1.63	**36**	**0.45**	361	3.53
Erigeron canadensis	0.214	**68**	**9.23**	**1,406**	**17.60**	3,302	32.29
Erigeron floribundus	0.000	6	0.81	10	0.13	51	0.50
Erigeron karvinskianus	1.000	0	0.00	3	0.04	6	0.06
Erigeron sumatrensis	0.000	5	0.68	**32**	**0.40**	359	3.51
Eucalyptus camaldulensis	1.000	0	0.00	1	0.01	5	0.05
Eucalyptus globulus	1.000	0	0.00	1	0.01	7	0.07
Euphorbia maculata	0.286	0	0.00	1	0.01	91	0.89
Euphorbia nutans	0.333	0	0.00	0	0.00	16	0.16
Euphorbia polygonifolia	0.000	0	0.00	6	0.08	7	0.07
Euphorbia prostrata	0.400	0	0.00	1	0.01	61	0.60
Euphorbia serpens	0.000	1	0.14	0	0.00	17	0.17
Euthamia graminifolia	1.000	0	0.00	1	0.01	1	0.01
Fraxinus americana	1.000	0	0.00	0	0.00	12	0.12
Fraxinus pennsylvanica	1.000	0	0.00	3	0.04	3	0.03
Freesia refracta	1.000	0	0.00	17	0.21	23	0.22
Galinsoga parviflora	0.091	1	0.14	13	0.16	167	1.63

Species name		Salinity		Oligotrophy		Drought	
	Pint	N	%	N	%	N	%
Galinsoga quadriradiata	0.111	0	0.00	3	0.04	51	0.50
Gaultheria procumbens	1.000	0	0.00	11	0.14	0	0.00
Gleditsia triacanthos	1.000	0	0.00	1	0.01	9	0.09
Glyceria striata	0.250	0	0.00	0	0.00	0	0.00
Gnaphalium coarctatum	0.000	0	0.00	0	0.00	0	0.00
Gomphocarpus fruticosus	1.000	0	0.00	3	0.04	6	0.06
Helianthus decapetalus	1.000	0	0.00	0	0.00	1	0.01
Helianthus tuberosus	0.900	0	0.00	4	0.05	95	0.93
Helianthus x laetiflorus	1.000	0	0.00	0	0.00	5	0.05
Heliotropium curassavicum	0.000	0	0.00	0	0.00	6	0.06
Hemerocallis fulva	1.000	0	0.00	0	0.00	0	0.00
Hordeum jubatum	1.000	1	0.14	0	0.00	1	0.01
Humulus japonicus	1.000	0	0.00	0	0.00	2	0.02
Impatiens balfourii	1.000	0	0.00	0	0.00	2	0.02
Impatiens capensis	1.000	0	0.00	1	0.01	0	0.00
Impatiens glandulifera	0.778	0	0.00	29	0.36	44	0.43
Impatiens parviflora	0.778	0	0.00	**577**	**7.22**	244	2.39
Ipomoea indica	1.000	0	0.00	0	0.00	1	0.01
Ipomoea purpurea	1.000	0	0.00	1	0.01	2	0.02
Iva xanthiifolia	0.000	0	0.00	0	0.00	11	0.11
Juglans nigra	1.000	0	0.00	3	0.04	5	0.05
Juncus tenuis	0.083	4	0.54	71	0.89	36	0.35
Larix kaempferi	1.000	0	0.00	76	0.95	0	0.00
Lepidium densiflorum	0.000	0	0.00	10	0.13	58	0.57
Lepidium didymum	0.286	8	1.09	5	0.06	45	0.44
Lepidium virginicum	0.143	0	0.00	19	0.24	83	0.81
Ligustrum japonicum	1.000	0	0.00	2	0.03	6	0.06
Ligustrum lucidum	1.000	0	0.00	2	0.03	8	0.08
Ligustrum ovalifolium	1.000	1	0.14	1	0.01	2	0.02
Lindernia dubia	0.000	0	0.00	0	0.00	0	0.00
Lonicera japonica	1.000	0	0.00	5	0.06	21	0.21
Lupinus arboreus	1.000	0	0.00	1	0.01	1	0.01
Lupinus polyphyllus	1.000	1	0.14	32	0.40	27	0.26

Species name	Pint	Salinity		Oligotrophy		Drought	
		N	%	N	%	N	%
Lycium barbarum	1.000	0	0.00	12	0.15	61	0.60
Lycopersicon esculentum	0.875	6	0.81	10	0.13	30	0.29
Mahonia aquifolium	1.000	0	0.00	7	0.09	12	0.12
Malus pumila	1.000	0	0.00	52	0.65	85	0.83
Matricaria discoidea	0.182	**14**	**1.90**	23	0.29	220	2.15
Mimulus guttatus	1.000	0	0.00	1	0.01	2	0.02
Mirabilis jalapa	1.000	0	0.00	0	0.00	14	0.14
Morus alba	1.000	0	0.00	4	0.05	14	0.14
Nicotiana glauca	1.000	2	0.27	4	0.05	17	0.17
Oenothera biennis	0.636	8	1.09	**389**	**4.87**	786	7.69
Oenothera drummondii	0.000	7	0.95	19	0.24	19	0.19
Oenothera oakesiana	0.200	8	1.09	46	0.58	55	0.54
Oenothera parviflora	0.250	4	0.54	3	0.04	11	0.11
Oenothera rosea	0.000	0	0.00	0	0.00	12	0.12
Oenothera strigosa	0.500	0	0.00	4	0.05	10	0.10
Opuntia ficus-indica	1.000	2	0.27	21	0.26	96	0.94
Opuntia stricta	1.000	5	0.68	7	0.09	11	0.11
Oryza sativa	1.000	0	0.00	0	0.00	0	0.00
Oxalis articulata	1.000	0	0.00	2	0.03	8	0.08
Oxalis corniculata	0.400	2	0.27	29	0.36	176	1.72
Oxalis debilis	0.500	0	0.00	0	0.00	3	0.03
Oxalis dillenii	0.250	0	0.00	45	0.56	51	0.50
Oxalis latifolia	0.250	0	0.00	0	0.00	5	0.05
Oxalis pes-caprae	0.625	6	0.81	**74**	**0.93**	555	5.43
Panicum capillare	0.333	0	0.00	3	0.04	66	0.65
Panicum dichotomiflorum	0.000	0	0.00	1	0.01	14	0.14
Parthenocissus quinquefolia	0.875	0	0.00	7	0.09	24	0.23
Paspalum dilatatum	0.500	3	0.41	3	0.04	31	0.30
Paspalum distichum	0.000	9	1.22	7	0.09	33	0.32
Paspalum vaginatum	0.250	**50**	**6.78**	8	0.10	42	0.41
Paulownia tomentosa	1.000	0	0.00	0	0.00	0	0.00
Phytolacca americana	1.000	0	0.00	22	0.28	16	0.16
Picea pungens	1.000	0	0.00	3	0.04	0	0.00

Species name	Pint	Salinity		Oligotrophy		Drought	
		N	%	N	%	N	%
Picea sitchensis	1.000	0	0.00	26	0.33	1	0.01
Pinus banksiana	1.000	0	0.00	9	0.11	2	0.02
Pinus radiata	1.000	0	0.00	7	0.09	6	0.06
Pinus strobus	1.000	0	0.00	84	1.05	0	0.00
Pittosporum tobira	1.000	0	0.00	1	0.01	9	0.09
Platanus occidentalis	1.000	0	0.00	0	0.00	1	0.01
Populus balsamifera	1.000	0	0.00	2	0.03	1	0.01
Populus carolinensis	1.000	0	0.00	1	0.01	3	0.03
Potentilla argyrophylla	1.000	0	0.00	9	0.11	0	0.00
Potentilla indica	0.600	0	0.00	6	0.08	3	0.03
Prunus serotina	1.000	0	0.00	**1,999**	**25.03**	95	0.93
Prunus virginiana	1.000	0	0.00	7	0.09	0	0.00
Pseudotsuga menziesii	1.000	0	0.00	**195**	**2.44**	10	0.10
Quercus palustris	1.000	0	0.00	2	0.03	0	0.00
Quercus rubra	1.000	0	0.00	**1,065**	**13.33**	37	0.36
Reynoutria japonica	0.818	0	0.00	11	0.14	35	0.34
Reynoutria sachalinensis	0.750	0	0.00	0	0.00	1	0.01
Rhapis excelsa	1.000	0	0.00	0	0.00	0	0.00
Ricinus communis	1.000	3	0.41	5	0.06	12	0.12
Robinia pseudoacacia	1.000	2	0.27	**479**	**6.00**	706	6.90
Rosa rugosa	1.000	0	0.00	14	0.18	16	0.16
Rudbeckia hirta	1.000	0	0.00	0	0.00	2	0.02
Rudbeckia laciniata	1.000	0	0.00	4	0.05	3	0.03
Senecio inaequidens	0.125	3	0.41	56	0.70	115	1.12
Setaria faberi	0.000	0	0.00	1	0.01	3	0.03
Sicyos angulatus	0.800	0	0.00	0	0.00	1	0.01
Sisyrinchium montanum	0.667	0	0.00	6	0.08	0	0.00
Solanum chenopodioides	0.000	1	0.14	0	0.00	10	0.10
Solanum linnaeanum	0.600	0	0.00	4	0.05	14	0.14
Solanum physalifolium	0.000	0	0.00	0	0.00	1	0.01
Solanum triflorum	0.000	0	0.00	0	0.00	5	0.05
Solidago altissima	1.000	0	0.00	0	0.00	2	0.02
Solidago canadensis	0.900	1	0.14	50	0.63	319	3.12

Species name	Pint	Salinity		Oligotrophy		Drought	
		N	%	N	%	N	%
Solidago gigantea	0.900	0	0.00	131	1.64	170	1.66
Soliva sessilis	0.000	0	0.00	4	0.05	5	0.05
Sorbaria sorbifolia	1.000	0	0.00	0	0.00	0	0.00
Spartina alterniflora	0.000	**36**	**4.88**	1	0.01	0	0.00
Spiraea japonica	1.000	0	0.00	0	0.00	0	0.00
Spiraea tomentosa	1.000	0	0.00	13	0.16	0	0.00
Sporobolus indicus	0.500	5	0.68	7	0.09	45	0.44
Sporobolus vaginiflorus	0.000	0	0.00	3	0.04	6	0.06
Stenotaphrum secundatum	0.667	**17**	**2.31**	11	0.14	20	0.20
Symphoricarpos albus	1.000	0	0.00	13	0.16	3	0.03
Symphyotrichum pilosum	1.000	0	0.00	0	0.00	5	0.05
Symphyotrichum squamatum	0.200	**113**	**15.33**	**33**	**0.41**	382	3.74
Tagetes minuta	0.000	0	0.00	0	0.00	5	0.05
Thladiantha dubia	1.000	0	0.00	10	0.13	0	0.00
Thuja occidentalis	1.000	0	0.00	0	0.00	0	0.00
Trachycarpus fortunei	1.000	0	0.00	0	0.00	0	0.00
Tradescantia fluminensis	1.000	0	0.00	0	0.00	2	0.02
Tropaeolum majus	0.800	0	0.00	0	0.00	3	0.03
Tsuga heterophylla	1.000	0	0.00	8	0.10	0	0.00
Vaccinium macrocarpon	0.500	0	0.00	49	0.61	6	0.06
Veronica peregrina	0.000	1	0.14	2	0.03	3	0.03
Veronica persica	0.091	2	0.27	68	0.85	333	3.26
Xanthium orientale	0.000	**251**	**34.06**	**488**	**6.11**	433	4.23
Xanthium spinosum	0.000	**17**	**2.31**	38	0.48	225	2.20
Yucca gloriosa	1.000	0	0.00	10	0.13	14	0.14
Zantedeschia aethiopica	1.000	0	0.00	0	0.00	2	0.02

(b) Habitats

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Abies grandis	1.000	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	15	0.06	0	0.00	0	0.00
Acacia dealbata	1.000	0	0.00	0	0.00	0	0.00	3	0.02	1	0.05	31	0.13	1	0.58	7	0.03
Acacia saligna	1.000	0	0.00	21	1.17	0	0.00	2	0.01	1	0.05	36	0.15	0	0.00	0	0.00
Acaena novae-zelandiae	0.000	0	0.00	4	0.22	0	0.00	12	0.07	0	0.00	1	0.00	0	0.00	0	0.00
Acalypha virginica	0.333	0	0.00	0	0.00	0	0.00	3	0.02	3	0.15	1	0.00	0	0.00	10	0.04
Acer negundo	0.909	0	0.00	1	0.06	21	0.70	84	0.52	34	1.70	**706**	**2.86**	0	0.00	129	0.46
Acorus calamus	0.889	0	0.00	1	0.06	**1,304**	**43.67**	258	1.61	8	0.40	41	0.17	0	0.00	2	0.01
Agave americana	1.000	0	0.00	21	1.17	0	0.00	4	0.02	7	0.35	19	0.08	0	0.00	2	0.01
Ageratina adenophora	0.500	0	0.00	0	0.00	0	0.00	5	0.03	0	0.00	10	0.04	0	0.00	3	0.01
Ailanthus altissima	1.000	0	0.00	3	0.17	1	0.03	29	0.18	23	1.15	215	0.87	3	1.74	103	0.37
Alternanthera caracasana	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	14	0.05
Amaranthus albus	0.222	0	0.00	0	0.00	2	0.07	24	0.15	7	0.35	8	0.03	2	1.16	**817**	**2.92**
Amaranthus blitoides	0.000	0	0.00	2	0.11	1	0.03	5	0.03	1	0.05	12	0.05	0	0.00	613	2.19
Amaranthus cruentus	1.000	0	0.00	0	0.00	0	0.00	3	0.02	2	0.10	4	0.02	0	0.00	64	0.23
Amaranthus deflexus	0.000	0	0.00	3	0.17	0	0.00	5	0.03	1	0.05	1	0.00	1	0.58	372	1.33
Amaranthus hybridus	0.143	0	0.00	0	0.00	0	0.00	18	0.11	2	0.10	8	0.03	1	0.58	**899**	**3.22**
Amaranthus hypochondriacus	1.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	1	0.00	0	0.00	45	0.16
Amaranthus muricatus	0.000	0	0.00	2	0.11	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	66	0.24
Amaranthus powellii	0.000	0	0.00	0	0.00	1	0.03	12	0.07	0	0.00	2	0.01	1	0.58	497	1.78

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Amaranthus retroflexus	0.091	0	0.00	4	0.22	22	0.74	178	1.11	14	0.70	37	0.15	**15**	**8.72**	**4,931**	**17.64**
Amaranthus viridis	0.000	0	0.00	1	0.06	2	0.07	5	0.03	0	0.00	0	0.00	0	0.00	90	0.32
Ambrosia artemisiifolia	0.000	0	0.00	3	0.17	4	0.13	194	1.21	13	0.65	28	0.11	3	1.74	**1,572**	**5.62**
Ambrosia psilostachya	0.000	1	0.32	**78**	**4.33**	0	0.00	9	0.06	0	0.00	3	0.01	0	0.00	34	0.12
Amorpha fruticosa	1.000	2	0.65	14	0.78	35	1.17	67	0.42	24	1.20	263	1.06	1	0.58	65	0.23
Apios americana	1.000	0	0.00	0	0.00	1	0.03	3	0.02	0	0.00	9	0.04	0	0.00	3	0.01
Arctotheca calendula	0.500	0	0.00	5	0.28	0	0.00	7	0.04	0	0.00	2	0.01	0	0.00	62	0.22
Aronia x prunifolia	1.000	0	0.00	0	0.00	16	0.54	6	0.04	7	0.35	44	0.18	0	0.00	0	0.00
Artemisia biennis	0.000	0	0.00	0	0.00	0	0.00	6	0.04	0	0.00	0	0.00	0	0.00	5	0.02
Artemisia verlotiorum	0.286	0	0.00	1	0.06	2	0.07	40	0.25	21	1.05	90	0.36	0	0.00	171	0.61
Asclepias syriaca	1.000	0	0.00	0	0.00	0	0.00	47	0.29	7	0.35	0	0.00	0	0.00	56	0.20
Baccharis halimifolia	1.000	**50**	**16.23**	20	1.11	3	0.10	23	0.14	5	0.25	7	0.03	0	0.00	6	0.02
Bidens aureus	0.000	0	0.00	0	0.00	0	0.00	25	0.16	0	0.00	0	0.00	0	0.00	30	0.11
Bidens bipinnatus	0.333	0	0.00	0	0.00	0	0.00	0	0.00	2	0.10	0	0.00	0	0.00	8	0.03
Bidens connatus	0.000	0	0.00	0	0.00	24	0.80	20	0.12	3	0.15	5	0.02	0	0.00	3	0.01
Bidens frondosus	0.182	0	0.00	5	0.28	**808**	**27.06**	**586**	**3.66**	**124**	**6.19**	**508**	**2.06**	2	1.16	362	1.30
Bidens subalternans	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	12	0.04
Bidens vulgatus	0.000	0	0.00	0	0.00	4	0.13	5	0.03	0	0.00	0	0.00	0	0.00	2	0.01
Buddleja davidii	1.000	1	0.32	0	0.00	0	0.00	35	0.22	17	0.85	63	0.25	2	1.16	31	0.11
Caragana arborescens	1.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	21	0.08	0	0.00	1	0.00

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Carpobrotus acinaciformis	1.000	0	0.00	**79**	**4.38**	0	0.00	2	0.01	13	0.65	4	0.02	0	0.00	8	0.03
Carpobrotus edulis	1.000	1	0.32	**141**	**7.82**	0	0.00	13	0.08	8	0.40	13	0.05	0	0.00	25	0.09
Cedrus atlantica	1.000	0	0.00	0	0.00	0	0.00	5	0.03	8	0.40	75	0.30	0	0.00	0	0.00
Celtis occidentalis	1.000	0	0.00	0	0.00	0	0.00	0	0.00	3	0.15	9	0.04	0	0.00	1	0.00
Cenchrus longisetus	1.000	0	0.00	0	0.00	0	0.00	5	0.03	0	0.00	0	0.00	0	0.00	5	0.02
Cenchrus longispinus	0.000	0	0.00	8	0.44	0	0.00	4	0.02	0	0.00	0	0.00	0	0.00	1	0.00
Cenchrus spinifex	0.000	0	0.00	33	1.83	0	0.00	2	0.01	0	0.00	5	0.02	0	0.00	10	0.04
Ceratochloa carinata	0.600	0	0.00	0	0.00	0	0.00	8	0.05	0	0.00	4	0.02	0	0.00	42	0.15
Ceratochloa cathartica	0.333	0	0.00	0	0.00	0	0.00	34	0.21	0	0.00	4	0.02	0	0.00	146	0.52
Chamaecyparis lawsoniana	1.000	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	11	0.04	0	0.00	1	0.00
Claytonia perfoliata	0.571	0	0.00	51	2.83	0	0.00	13	0.08	24	1.20	9	0.04	0	0.00	68	0.24
Claytonia sibirica	1.000	0	0.00	0	0.00	0	0.00	5	0.03	0	0.00	7	0.03	0	0.00	0	0.00
Collomia grandiflora	1.000	0	0.00	0	0.00	0	0.00	15	0.09	0	0.00	0	0.00	0	0.00	8	0.03
Cornus sericea	1.000	0	0.00	0	0.00	2	0.07	2	0.01	4	0.20	43	0.17	0	0.00	2	0.01
Cortaderia selloana	1.000	**9**	**2.92**	3	0.17	0	0.00	39	0.24	1	0.05	4	0.02	0	0.00	8	0.03
Cotoneaster horizontalis	1.000	0	0.00	0	0.00	0	0.00	1	0.01	1	0.05	12	0.05	0	0.00	1	0.00
Cotoneaster lucidus	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	64	0.26	0	0.00	0	0.00
Cotula australis	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	14	0.05
Cotula coronopifolia	0.222	**39**	**12.66**	2	0.11	10	0.33	42	0.26	4	0.20	0	0.00	0	0.00	16	0.06
Crassula lycopodioides	1.000	0	0.00	0	0.00	0	0.00	219	1.37	1	0.05	0	0.00	3	1.74	27	0.10

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Cuscuta campestris	0.000	1	0.32	9	0.50	0	0.00	27	0.17	6	0.30	6	0.02	0	0.00	73	0.26
Cyperus eragrostis	0.000	1	0.32	0	0.00	24	0.80	161	1.01	21	1.05	56	0.23	0	0.00	50	0.18
Datura stramonium	0.667	0	0.00	5	0.28	0	0.00	20	0.12	7	0.35	20	0.08	0	0.00	775	2.77
Deutzia scabra	1.000	0	0.00	0	0.00	0	0.00	0	0.00	4	0.20	11	0.04	0	0.00	0	0.00
Dichondra micrantha	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	13	0.05
Dysphania ambrosioides	0.700	1	0.32	5	0.28	2	0.07	30	0.19	14	0.70	17	0.07	0	0.00	204	0.73
Dysphania multifida	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	22	0.08
Dysphania pumilio	0.000	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	14	0.05
Echinochloa oryzoides	0.000	0	0.00	0	0.00	8	0.27	2	0.01	0	0.00	0	0.00	0	0.00	36	0.13
Echinocystis lobata	1.000	0	0.00	0	0.00	14	0.47	169	1.06	51	2.54	110	0.45	1	0.58	51	0.18
Elaeagnus pungens	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	11	0.04	0	0.00	0	0.00
Eleusine tristachya	0.000	0	0.00	0	0.00	0	0.00	5	0.03	0	0.00	0	0.00	0	0.00	9	0.03
Epilobium brachycarpum	0.000	0	0.00	0	0.00	0	0.00	3	0.02	0	0.00	0	0.00	**4**	**2.33**	45	0.16
Epilobium brunnescens	0.500	0	0.00	0	0.00	4	0.13	69	0.43	0	0.00	3	0.01	0	0.00	0	0.00
Epilobium ciliatum	0.000	2	0.65	4	0.22	**214**	**7.17**	**926**	**5.78**	60	2.99	214	0.87	**10**	**5.81**	437	1.56
Eragrostis pectinacea	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	13	0.05
Eragrostis virescens	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	10	0.04
Erechtites hieraciifolius	0.000	0	0.00	0	0.00	1	0.03	8	0.05	1	0.05	45	0.18	0	0.00	10	0.04
Erigeron annuus	0.364	0	0.00	1	0.06	33	1.11	**2,233**	**13.94**	**172**	**8.58**	**533**	**2.16**	**15**	**8.72**	**1,634**	**5.85**

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Erigeron bonariensis	0.000	3	0.97	17	0.94	1	0.03	53	0.33	3	0.15	56	0.23	**7**	**4.07**	589	2.11
Erigeron canadensis	0.214	**34**	**11.04**	**179**	**9.93**	**59**	**1.98**	**3,274**	**20.44**	**219**	**10.93**	461	1.87	**64**	**37.21**	**6,933**	**24.81**
Erigeron floribundus	0.000	4	1.30	10	0.55	1	0.03	60	0.37	0	0.00	11	0.04	0	0.00	99	0.35
Erigeron karvinskianus	1.000	0	0.00	0	0.00	0	0.00	6	0.04	0	0.00	1	0.00	**5**	**2.91**	36	0.13
Erigeron sumatrensis	0.000	1	0.32	13	0.72	1	0.03	59	0.37	8	0.40	72	0.29	**8**	**4.65**	556	1.99
Eucalyptus camaldulensis	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	17	0.07	0	0.00	4	0.01
Eucalyptus globulus	1.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	24	0.10	0	0.00	3	0.01
Euphorbia maculata	0.286	0	0.00	0	0.00	1	0.03	7	0.04	3	0.15	0	0.00	0	0.00	119	0.43
Euphorbia nutans	0.333	0	0.00	0	0.00	0	0.00	3	0.02	1	0.05	0	0.00	0	0.00	35	0.13
Euphorbia polygonifolia	0.000	0	0.00	9	0.50	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.00
Euphorbia prostrata	0.400	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	4	0.02	1	0.58	114	0.41
Euphorbia serpens	0.000	1	0.32	0	0.00	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	31	0.11
Euthamia graminifolia	1.000	0	0.00	0	0.00	2	0.07	9	0.06	0	0.00	0	0.00	0	0.00	2	0.01
Fraxinus americana	1.000	0	0.00	0	0.00	0	0.00	0	0.00	2	0.10	51	0.21	0	0.00	1	0.00
Fraxinus pennsylvanica	1.000	0	0.00	0	0.00	1	0.03	5	0.03	2	0.10	61	0.25	0	0.00	1	0.00
Freesia refracta	1.000	0	0.00	0	0.00	0	0.00	2	0.01	3	0.15	20	0.08	0	0.00	1	0.00
Galinsoga parviflora	0.091	0	0.00	1	0.06	7	0.23	219	1.37	15	0.75	46	0.19	**7**	**4.07**	**3,625**	**12.97**

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Galinsoga quadriradiata	0.111	0	0.00	0	0.00	6	0.20	145	0.91	5	0.25	26	0.11	2	1.16	**1,393**	**4.98**
Gaultheria procumbens	1.000	0	0.00	0	0.00	0	0.00	6	0.04	7	0.35	0	0.00	0	0.00	0	0.00
Gleditsia triacanthos	1.000	0	0.00	0	0.00	1	0.03	3	0.02	0	0.00	25	0.10	0	0.00	9	0.03
Glyceria striata	0.250	0	0.00	0	0.00	0	0.00	15	0.09	0	0.00	2	0.01	0	0.00	0	0.00
Gnaphalium coarctatum	0.000	0	0.00	0	0.00	0	0.00	10	0.06	0	0.00	0	0.00	0	0.00	3	0.01
Gomphocarpus fruticosus	1.000	0	0.00	1	0.06	0	0.00	3	0.02	9	0.45	3	0.01	0	0.00	4	0.01
Helianthus decapetalus	1.000	0	0.00	0	0.00	0	0.00	3	0.02	0	0.00	0	0.00	0	0.00	8	0.03
Helianthus tuberosus	0.900	0	0.00	0	0.00	3	0.10	114	0.71	36	1.80	129	0.52	1	0.58	416	1.49
Helianthus x laetiflorus	1.000	0	0.00	0	0.00	1	0.03	7	0.04	0	0.00	4	0.02	0	0.00	15	0.05
Heliotropium curassavicum	0.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	10	0.04
Hemerocallis fulva	1.000	0	0.00	0	0.00	0	0.00	4	0.02	2	0.10	44	0.18	0	0.00	1	0.00
Hordeum jubatum	1.000	0	0.00	0	0.00	1	0.03	5	0.03	0	0.00	7	0.03	0	0.00	4	0.01
Humulus japonicus	1.000	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	7	0.03	0	0.00	8	0.03
Impatiens balfourii	1.000	0	0.00	0	0.00	0	0.00	14	0.09	0	0.00	12	0.05	0	0.00	6	0.02
Impatiens capensis	1.000	0	0.00	0	0.00	15	0.50	8	0.05	1	0.05	14	0.06	0	0.00	0	0.00
Impatiens glandulifera	0.778	0	0.00	3	0.17	**55**	**1.84**	**783**	**4.89**	**135**	**6.74**	**1,040**	**4.21**	1	0.58	179	0.64
Impatiens parviflora	0.778	0	0.00	5	0.28	**60**	**2.01**	**1,017**	**6.35**	**281**	**14.02**	**7,832**	**31.69**	**14**	**8.14**	537	1.92
Ipomoea indica	1.000	0	0.00	0	0.00	0	0.00	5	0.03	0	0.00	2	0.01	0	0.00	5	0.02

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Ipomoea purpurea	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.58	9	0.03
Iva xanthiifolia	0.000	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00	74	0.26
Juglans nigra	1.000	0	0.00	0	0.00	0	0.00	3	0.02	0	0.00	57	0.23	0	0.00	1	0.00
Juncus tenuis	0.083	1	0.32	0	0.00	**42**	**1.41**	**1,004**	**6.27**	23	1.15	112	0.45	0	0.00	144	0.52
Larix kaempferi	1.000	0	0.00	0	0.00	0	0.00	5	0.03	2	0.10	455	1.84	0	0.00	0	0.00
Lepidium densiflorum	0.000	0	0.00	0	0.00	0	0.00	18	0.11	0	0.00	5	0.02	1	0.58	117	0.42
Lepidium didymum	0.286	0	0.00	4	0.22	1	0.03	21	0.13	1	0.05	1	0.00	0	0.00	257	0.92
Lepidium virginicum	0.143	0	0.00	0	0.00	0	0.00	30	0.19	0	0.00	0	0.00	0	0.00	158	0.57
Ligustrum japonicum	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	9	0.04	0	0.00	3	0.01
Ligustrum lucidum	1.000	0	0.00	4	0.22	0	0.00	0	0.00	1	0.05	16	0.06	0	0.00	1	0.00
Ligustrum ovalifolium	1.000	0	0.00	3	0.17	0	0.00	1	0.01	3	0.15	5	0.02	0	0.00	1	0.00
Lindernia dubia	0.000	0	0.00	0	0.00	4	0.13	4	0.02	0	0.00	0	0.00	0	0.00	19	0.07
Lonicera japonica	1.000	0	0.00	8	0.44	6	0.20	9	0.06	12	0.60	96	0.39	0	0.00	10	0.04
Lupinus arboreus	1.000	0	0.00	3	0.17	0	0.00	6	0.04	0	0.00	0	0.00	0	0.00	1	0.00
Lupinus polyphyllus	1.000	0	0.00	0	0.00	1	0.03	189	1.18	10	0.50	48	0.19	1	0.58	38	0.14
Lycium barbarum	1.000	0	0.00	1	0.06	0	0.00	26	0.16	14	0.70	19	0.08	2	1.16	114	0.41
Lycopersicon esculentum	0.875	1	0.32	7	0.39	8	0.27	61	0.38	6	0.30	17	0.07	1	0.58	247	0.88
Mahonia aquifolium	1.000	0	0.00	0	0.00	0	0.00	4	0.02	5	0.25	68	0.28	0	0.00	5	0.02
Malus pumila	1.000	0	0.00	2	0.11	0	0.00	61	0.38	20	1.00	325	1.31	0	0.00	33	0.12
Matricaria discoidea	0.182	**12**	**3.90**	5	0.28	15	0.50	**1,506**	**9.40**	7	0.35	24	0.10	**6**	**3.49**	**4,080**	**14.60**
Mimulus guttatus	1.000	0	0.00	0	0.00	25	0.84	66	0.41	2	0.10	6	0.02	1	0.58	9	0.03
Mirabilis jalapa	1.000	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	1	0.00	0	0.00	44	0.16
Morus alba	1.000	0	0.00	2	0.11	0	0.00	9	0.06	9	0.45	138	0.56	0	0.00	10	0.04
Nicotiana glauca	1.000	0	0.00	3	0.17	0	0.00	2	0.01	2	0.10	2	0.01	0	0.00	17	0.06

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Oenothera biennis	0.636	7	2.27	**145**	**8.05**	4	0.13	**576**	**3.60**	36	1.80	72	0.29	**11**	**6.40**	580	2.08
Oenothera drummondii	0.000	0	0.00	21	1.17	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Oenothera oakesiana	0.200	7	2.27	**67**	**3.72**	0	0.00	27	0.17	1	0.05	0	0.00	0	0.00	13	0.05
Oenothera parviflora	0.250	2	0.65	4	0.22	1	0.03	15	0.09	0	0.00	0	0.00	0	0.00	16	0.06
Oenothera rosea	0.000	0	0.00	0	0.00	0	0.00	14	0.09	1	0.05	0	0.00	0	0.00	20	0.07
Oenothera strigosa	0.500	0	0.00	0	0.00	0	0.00	6	0.04	0	0.00	0	0.00	0	0.00	6	0.02
Opuntia ficus-indica	1.000	0	0.00	9	0.50	0	0.00	13	0.08	41	2.05	35	0.14	0	0.00	14	0.05
Opuntia stricta	1.000	0	0.00	6	0.33	0	0.00	4	0.02	5	0.25	3	0.01	0	0.00	0	0.00
Oryza sativa	1.000	0	0.00	0	0.00	11	0.37	1	0.01	0	0.00	0	0.00	0	0.00	81	0.29
Oxalis articulata	1.000	0	0.00	0	0.00	0	0.00	4	0.02	0	0.00	4	0.02	0	0.00	30	0.11
Oxalis corniculata	0.400	0	0.00	11	0.61	0	0.00	67	0.42	5	0.25	94	0.38	0	0.00	394	1.41
Oxalis debilis	0.500	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	3	0.01	0	0.00	7	0.03
Oxalis dillenii	0.250	0	0.00	0	0.00	0	0.00	73	0.46	0	0.00	3	0.01	0	0.00	69	0.25
Oxalis latifolia	0.250	0	0.00	0	0.00	0	0.00	11	0.07	0	0.00	4	0.02	0	0.00	103	0.37
Oxalis pes-caprae	0.625	2	0.65	18	1.00	0	0.00	54	0.34	**77**	**3.84**	196	0.79	0	0.00	599	2.14
Panicum capillare	0.333	0	0.00	0	0.00	1	0.03	36	0.22	0	0.00	3	0.01	1	0.58	205	0.73
Panicum dichotomiflorum	0.000	0	0.00	0	0.00	0	0.00	17	0.11	0	0.00	4	0.02	0	0.00	97	0.35
Parthenocissus quinquefolia	0.875	0	0.00	5	0.28	1	0.03	36	0.22	20	1.00	130	0.53	3	1.74	60	0.21
Paspalum dilatatum	0.500	2	0.65	0	0.00	2	0.07	207	1.29	2	0.10	4	0.02	0	0.00	65	0.23
Paspalum distichum	0.000	5	1.62	6	0.33	**95**	**3.18**	188	1.17	21	1.05	54	0.22	0	0.00	145	0.52

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Paspalum vaginatum	0.250	**45**	**14.61**	14	0.78	10	0.33	40	0.25	2	0.10	0	0.00	0	0.00	80	0.29
Paulownia tomentosa	1.000	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	13	0.05	0	0.00	0	0.00
Phytolacca americana	1.000	0	0.00	1	0.06	1	0.03	9	0.06	11	0.55	114	0.46	1	0.58	28	0.10
Picea pungens	1.000	0	0.00	0	0.00	0	0.00	6	0.04	1	0.05	7	0.03	0	0.00	0	0.00
Picea sitchensis	1.000	0	0.00	5	0.28	0	0.00	60	0.37	0	0.00	192	0.78	1	0.58	0	0.00
Pinus banksiana	1.000	0	0.00	1	0.06	0	0.00	5	0.03	0	0.00	13	0.05	0	0.00	0	0.00
Pinus radiata	1.000	0	0.00	0	0.00	0	0.00	3	0.02	1	0.05	31	0.13	0	0.00	3	0.01
Pinus strobus	1.000	0	0.00	2	0.11	0	0.00	10	0.06	3	0.15	285	1.15	0	0.00	0	0.00
Pittosporum tobira	1.000	0	0.00	1	0.06	0	0.00	2	0.01	2	0.10	9	0.04	0	0.00	3	0.01
Platanus occidentalis	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	13	0.05	0	0.00	1	0.00
Populus balsamifera	1.000	0	0.00	3	0.17	0	0.00	3	0.02	2	0.10	19	0.08	0	0.00	0	0.00
Populus carolinensis	1.000	0	0.00	1	0.06	0	0.00	5	0.03	2	0.10	8	0.03	0	0.00	4	0.01
Potentilla argyrophylla	1.000	0	0.00	0	0.00	0	0.00	3	0.02	7	0.35	1	0.00	0	0.00	0	0.00
Potentilla indica	0.600	0	0.00	0	0.00	0	0.00	16	0.10	11	0.55	74	0.30	2	1.16	8	0.03
Prunus serotina	1.000	0	0.00	**140**	**7.77**	3	0.10	337	2.10	**198**	**9.88**	**5,577**	**22.56**	2	1.16	30	0.11
Prunus virginiana	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	21	0.08	0	0.00	0	0.00
Pseudotsuga menziesii	1.000	0	0.00	0	0.00	0	0.00	19	0.12	9	0.45	**1,066**	**4.31**	1	0.58	5	0.02
Quercus palustris	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	22	0.09	0	0.00	0	0.00
Quercus rubra	1.000	0	0.00	16	0.89	2	0.07	118	0.74	**67**	**3.34**	**3,771**	**15.26**	0	0.00	12	0.04
Reynoutria japonica	0.818	0	0.00	1	0.06	1	0.03	82	0.51	27	1.35	228	0.92	2	1.16	357	1.28
Reynoutria sachalinensis	0.750	0	0.00	0	0.00	0	0.00	4	0.02	0	0.00	11	0.04	0	0.00	34	0.12

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Rhapis excelsa	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	10	0.04	0	0.00	0	0.00
Ricinus communis	1.000	0	0.00	5	0.28	0	0.00	2	0.01	1	0.05	1	0.00	0	0.00	14	0.05
Robinia pseudoacacia	1.000	0	0.00	23	1.28	3	0.10	301	1.88	**119**	**5.94**	**4,296**	**17.38**	**6**	**3.49**	318	1.14
Rosa rugosa	1.000	0	0.00	42	2.33	0	0.00	26	0.16	8	0.40	13	0.05	0	0.00	15	0.05
Rudbeckia hirta	1.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	4	0.02	0	0.00	5	0.02
Rudbeckia laciniata	1.000	0	0.00	0	0.00	9	0.30	73	0.46	13	0.65	97	0.39	0	0.00	52	0.19
Senecio inaequidens	0.125	1	0.32	**55**	**3.05**	0	0.00	88	0.55	16	0.80	31	0.13	2	1.16	109	0.39
Setaria faberi	0.000	0	0.00	0	0.00	0	0.00	11	0.07	0	0.00	1	0.00	0	0.00	42	0.15
Sicyos angulatus	0.800	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	14	0.06	0	0.00	10	0.04
Sisyrinchium montanum	0.667	0	0.00	0	0.00	1	0.03	24	0.15	0	0.00	0	0.00	0	0.00	0	0.00
Solanum chenopodioides	0.000	1	0.32	0	0.00	0	0.00	14	0.09	1	0.05	16	0.06	0	0.00	20	0.07
Solanum linnaeanum	0.600	0	0.00	7	0.39	0	0.00	0	0.00	1	0.05	2	0.01	0	0.00	7	0.03
Solanum physalifolium	0.000	0	0.00	0	0.00	2	0.07	0	0.00	0	0.00	0	0.00	0	0.00	12	0.04
Solanum triflorum	0.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	0	0.00	0	0.00	16	0.06
Solidago altissima	1.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	1	0.00	0	0.00	7	0.03
Solidago canadensis	0.900	0	0.00	0	0.00	9	0.30	568	3.55	**67**	**3.34**	249	1.01	3	1.74	539	1.93
Solidago gigantea	0.900	0	0.00	0	0.00	**103**	**3.45**	**1,073**	**6.70**	**188**	**9.38**	**1,212**	**4.90**	**6**	**3.49**	465	1.66
Soliva sessilis	0.000	0	0.00	0	0.00	0	0.00	3	0.02	0	0.00	3	0.01	0	0.00	7	0.03
Sorbaria sorbifolia	1.000	0	0.00	0	0.00	0	0.00	1	0.01	0	0.00	17	0.07	0	0.00	2	0.01
Spartina alterniflora	0.000	**35**	**11.36**	2	0.11	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00

Species name	Pint	Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
		N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Spiraea japonica	1.000	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	10	0.04	0	0.00	0	0.00
Spiraea tomentosa	1.000	0	0.00	0	0.00	13	0.44	4	0.02	0	0.00	0	0.00	0	0.00	0	0.00
Sporobolus indicus	0.500	5	1.62	2	0.11	0	0.00	98	0.61	0	0.00	12	0.05	0	0.00	70	0.25
Sporobolus vaginiflorus	0.000	0	0.00	0	0.00	0	0.00	10	0.06	0	0.00	0	0.00	0	0.00	6	0.02
Stenotaphrum secundatum	0.667	**15**	**4.87**	14	0.78	1	0.03	46	0.29	0	0.00	6	0.02	0	0.00	18	0.06
Symphoricarpos albus	1.000	0	0.00	3	0.17	0	0.00	12	0.07	12	0.60	189	0.76	0	0.00	22	0.08
Symphyotrichum pilosum	1.000	0	0.00	0	0.00	0	0.00	1	0.01	1	0.05	3	0.01	0	0.00	12	0.04
Symphyotrichum squamatum	0.200	**82**	**26.62**	21	1.17	33	1.11	302	1.89	21	1.05	99	0.40	**7**	**4.07**	672	2.40
Tagetes minuta	0.000	0	0.00	0	0.00	0	0.00	2	0.01	0	0.00	0	0.00	0	0.00	15	0.05
Thladiantha dubia	1.000	0	0.00	0	0.00	0	0.00	7	0.04	6	0.30	12	0.05	0	0.00	5	0.02
Thuja occidentalis	1.000	0	0.00	0	0.00	0	0.00	1	0.01	1	0.05	8	0.03	0	0.00	1	0.00
Trachycarpus fortunei	1.000	0	0.00	0	0.00	0	0.00	0	0.00	1	0.05	9	0.04	0	0.00	0	0.00
Tradescantia fluminensis	1.000	0	0.00	0	0.00	0	0.00	6	0.04	4	0.20	20	0.08	0	0.00	4	0.01
Tropaeolum majus	0.800	0	0.00	0	0.00	0	0.00	7	0.04	0	0.00	0	0.00	0	0.00	6	0.02
Tsuga heterophylla	1.000	0	0.00	0	0.00	0	0.00	1	0.01	1	0.05	31	0.13	0	0.00	0	0.00
Vaccinium macrocarpon	0.500	0	0.00	**68**	**3.77**	6	0.20	2	0.01	15	0.75	4	0.02	0	0.00	0	0.00
Veronica peregrina	0.000	0	0.00	0	0.00	6	0.20	26	0.16	0	0.00	1	0.00	0	0.00	37	0.13
Veronica persica	0.091	2	0.65	4	0.22	3	0.10	511	3.19	21	1.05	65	0.26	**8**	**4.65**	**7,003**	**25.06**

Species name		Littoral		Coastal		Wetlands		Grasslands		Scrub		Forest		LittleSoil		ManMade	
	Pint	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Xanthium orientale	0.000	**22**	**7.14**	**549**	**30.47**	**87**	**2.91**	258	1.61	29	1.45	82	0.33	0	0.00	544	1.95
Xanthium spinosum	0.000	0	0.00	18	1.00	2	0.07	78	0.49	4	0.20	14	0.06	0	0.00	753	2.69
Yucca gloriosa	1.000	0	0.00	12	0.67	0	0.00	2	0.01	0	0.00	1	0.00	0	0.00	1	0.00
Zantedeschia aethiopica	1.000	0	0.00	0	0.00	0	0.00	8	0.05	0	0.00	7	0.03	0	0.00	3	0.01

Table S3.7. Introduction pathways shape niche harshness across Europe. Environmental drivers of the mean intentionality proportion of invaded plots across Europe. Model-averaged coefficients and relative importance (standardized general dominance) from Generalized Linear Mixed Models. Abbreviations: CI = Confidence interval, Rel. Imp = Relative importance.

Variable	Coefficient	Lower.CI	Upper.CI	Rel. Imp
Intercept	-0.607	-0.833	-0.381	
Drought: Yes	0.326	0.263	0.388	0.0064
Salinity: Yes	-1.076	-1.338	-0.814	0.0055
Oligotrophy: Yes	0.062	-0.029	0.153	0.0210
Elevation (linear)	-0.103	-0.139	-0.068	0.0126
Elevation (quadratic)	0.004	-0.005	0.013	
Habitat: Man-made	-0.697	-0.831	-0.563	0.8252
Habitat: Little soil, sparse vegetation	-0.278	-0.628	0.071	
Habitat: Grasslands	0.137	0.007	0.266	
Habitat: Littoral biogenic	0.625	0.269	0.980	
Habitat: Wetlands	0.714	0.566	0.862	
Habitat: Heathlands, scrub and tundra	1.168	1.012	1.323	
Habitat: Forests	2.184	2.052	2.316	
Annual precipitation (linear)	0.142	0.107	0.178	0.0106
Annual precipitation (quadratic)	-0.018	-0.028	-0.009	
Cropland land-cover (linear only)	-0.125	-0.147	-0.103	0.0496
Urban land-cover (linear)	-0.002	-0.024	0.020	0.0304
Urban land-cover (quadratic)	-0.001	-0.013	0.010	
Longitude (linear)	-0.046	-0.115	0.022	0.0385
Longitude (quadratic)	-0.050	-0.081	-0.018	
Latitude (linear)	-0.054	-0.111	0.003	0.0001
Latitude (quadratic)	0.058	0.035	0.081	

Table S3.8. Estimated marginal means and trends (model-averaged), of the environmental drivers of the mean intentionality proportion of invaded plots across Europe. Different letters indicate significantly different means (Tukey contrast). Abbreviations: CI = Confidence interval, cld = compact letter display.

Variable	Level or degree	Estimate	Lower CI	Upper CI	cld
Drought	No	0.369	0.329	0.408	a
Drought	Yes	0.433	0.390	0.476	b
Salinity	No	0.509	0.466	0.552	b
Salinity	Yes	0.293	0.241	0.345	a
Oligotrophy	No	0.395	0.353	0.436	a
Oligotrophy	Yes	0.407	0.365	0.449	a
Elevation	linear	-0.020	-0.027	-0.013	
Elevation	quadratic	0.001	-0.001	0.003	
Habitat	Man-made	0.176	0.146	0.205	a
Habitat	Little soil, sparse vegetation	0.241	0.173	0.308	ab
Habitat	Coastal	0.292	0.248	0.336	b
Habitat	Grasslands	0.319	0.275	0.363	bc
Habitat	Littoral biogenic	0.425	0.346	0.503	cde
Habitat	Wetlands	0.445	0.391	0.499	d
Habitat	Heathlands, scrub and tundra	0.550	0.492	0.607	e
Habitat	Forests	0.760	0.716	0.803	f
Annual precipitation	linear	0.028	0.021	0.035	
Annual precipitation	quadratic	-0.003	-0.005	-0.001	
Cropland	linear	-0.025	-0.029	-0.020	
Urban	linear	0.000	-0.005	0.004	
Urban	quadratic	0.000	-0.003	0.002	
Longitude	linear	-0.009	-0.022	0.004	
Longitude	quadratic	-0.010	-0.016	-0.003	
Latitude	linear	-0.011	-0.022	0.000	
Latitude	quadratic	0.011	0.007	0.016	

Table S3.9. Pairwise covariation among introduction pathways, plant traits and minimum residence time, assessed for two datasets: **(a)** a dataset without duplicates (used for models coding pathways as 3 categories [intentional, unintentional, both] and as intentionality proportion), **(b)** a dataset with duplicates (62 neophytes introduced through both pathways are duplicated, used for models coding pathways as 2 categories [intentional, unintentional]. Although intentionality proportion was not modelled using these duplicate dataset, we have included it to show covariation between alternative ways to code introduction pathways). In all cases, covariation between variables was assessed through calculation of effect size and a significance test: Pearson's correlation and t-test for continuous x continuous, Cramér's V and Chi-square for categorical x categorical, and R^2 and ANOVA (Analysis of variance) for continuous x categorical. The tables rank covariation in absolute value, from greatest to lowest (all metrics of effect size had a theoretical range 0-1 in absolute value).

(a) Dataset without duplicates

Variable 1	Variable 2	Effect size metric	Effect size value	Significance test	Significance p-v
Pathway: Intentionality proportion	Pathway: Intent. + Unint., Intent., Unint.	R^2	0.900	ANOVA	0.000
Growth form	Pathway: Intent. + Unint., Intent., Unint.	Cramer's V	0.480	Chi-square	0.000
Pathway: Intentionality proportion	Growth form	R^2	0.418	ANOVA	0.000
Height	Pathway: Intentionality proportion	Pearson's correlation	0.393	t-test	0.000
Growth form	Dispersal syndrome	Cramer's V	0.392	Chi-square	0.000
Height	Growth form	R^2	0.354	ANOVA	0.000
Dispersal syndrome	Pathway: Intent. + Unint., Intent., Unint.	Cramer's V	0.334	Chi-square	0.000
Native climatic niche breadth	Height	Pearson's correlation	-0.293	t-test	0.000
Native climatic niche breadth	Pathway: Intentionality proportion	Pearson's correlation	-0.290	t-test	0.000
Pathway: Intentionality proportion	Dispersal syndrome	R^2	0.193	ANOVA	0.000
Height	Pathway: Intent. + Unint., Intent., Unint.	R^2	0.175	ANOVA	0.000
Native climatic niche breadth	Growth form	R^2	0.127	ANOVA	0.000
Height	Dispersal syndrome	R^2	0.125	ANOVA	0.000

Variable 1	Variable 2	Effect size metric	Effect size value	Significance test	Significance p-v
Minimum residence time	Pathway: Intent. + Unint., Intent., Unint.	R^2	0.115	ANOVA	0.000
Native climatic niche breadth	Pathway: Intent. + Unint., Intent., Unint.	R^2	0.113	ANOVA	0.000
Minimum residence time	Pathway: Intentionality proportion	Pearson's correlation	0.081	t-test	0.232
Minimum residence time	Height	Pearson's correlation	0.045	t-test	0.506
Native climatic niche breadth	Minimum residence time	Pearson's correlation	0.039	t-test	0.566
Minimum residence time	Dispersal syndrome	R^2	0.024	ANOVA	0.157
Native climatic niche breadth	Dispersal syndrome	R^2	0.018	ANOVA	0.279
Minimum residence time	Growth form	R^2	0.002	ANOVA	0.837

(b) Dataset with duplicates

Variable 1	Variable 2	Effect size metric	Effect size value	Significance test	Significance p-v
Growth form	Pathway: Intent., Unint.	Cramer's V	0.450	Chi-square	0.000
Pathway: Intentionality proportion	Pathway: Intent., Unint.	R^2	0.446	ANOVA	0.000
Height	Pathway: Intentionality proportion	Pearson's correlation	0.404	t-test	0.000
Growth form	Dispersal syndrome	Cramer's V	0.393	Chi-square	0.000
Pathway: Intentionality proportion	Growth form	R^2	0.378	ANOVA	0.000
Height	Growth form	R^2	0.347	ANOVA	0.000
Dispersal syndrome	Pathway: Intent., Unint.	Cramer's V	0.297	Chi-square	0.000
Native climatic niche breadth	Height	Pearson's correlation	-0.283	t-test	0.000
Native climatic niche breadth	Pathway: Intentionality proportion	Pearson's correlation	-0.270	t-test	0.000
Pathway: Intentionality proportion	Dispersal syndrome	R^2	0.176	ANOVA	0.000
Native climatic niche breadth	Growth form	R^2	0.122	ANOVA	0.000
Height	Dispersal syndrome	R^2	0.108	ANOVA	0.000
Height	Pathway: Intent., Unint.	R^2	0.085	ANOVA	0.000
Minimum residence time	Pathway: Intentionality proportion	Pearson's correlation	0.054	t-test	0.368
Native climatic niche breadth	Minimum residence time	Pearson's correlation	0.050	t-test	0.403
Native climatic niche breadth	Pathway: Intent., Unint.	R^2	0.041	ANOVA	0.001
Native climatic niche breadth	Dispersal syndrome	R^2	0.023	ANOVA	0.086
Minimum residence time	Dispersal syndrome	R^2	0.022	ANOVA	0.104
Minimum residence time	Height	Pearson's correlation	0.011	t-test	0.848
Minimum residence time	Growth form	R^2	0.002	ANOVA	0.739
Minimum residence time	Pathway: Intent., Unint.	R^2	0.001	ANOVA	0.659

Supplementary figures

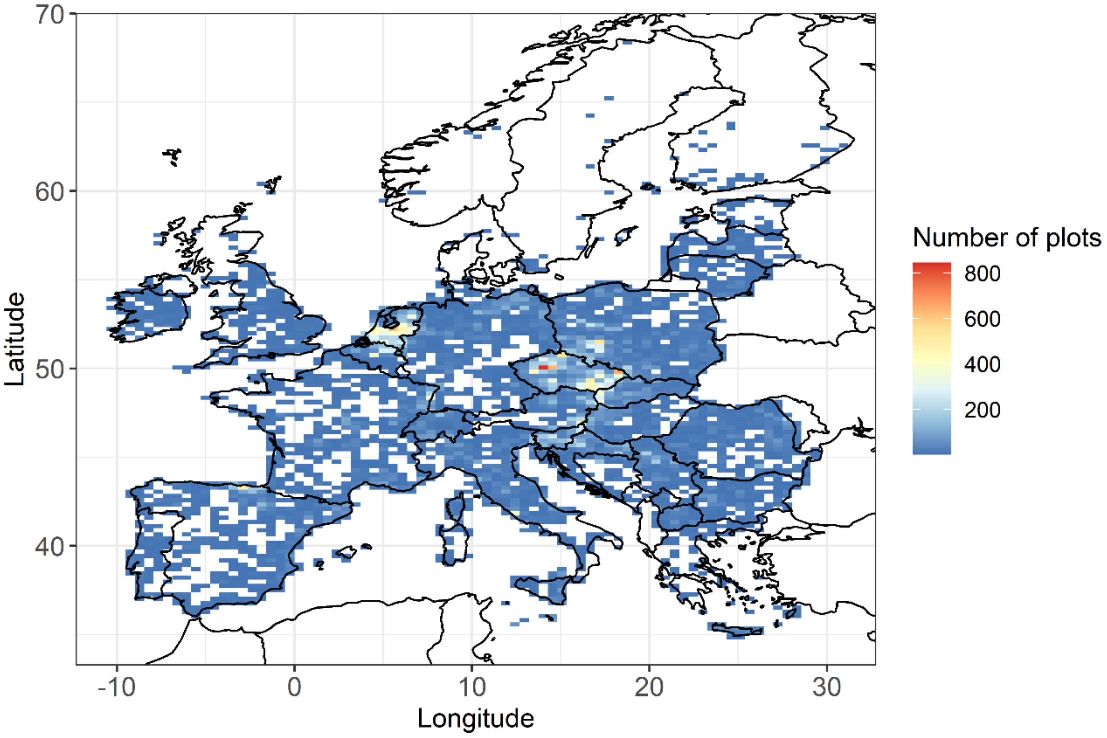


Fig. S3.1. Distribution of invaded vegetation plots across Europe Number of vegetation plots across regular rectangles, obtained using ‘ggplot2’ package (Wickham, 2016), in particular: ‘geom_bin2d(bins = 700)’. Country outlines were taken from ‘map_data(“world”)’, form the ‘ggplot2’ package (Wickham, 2016). N = 75,957 invaded plots.

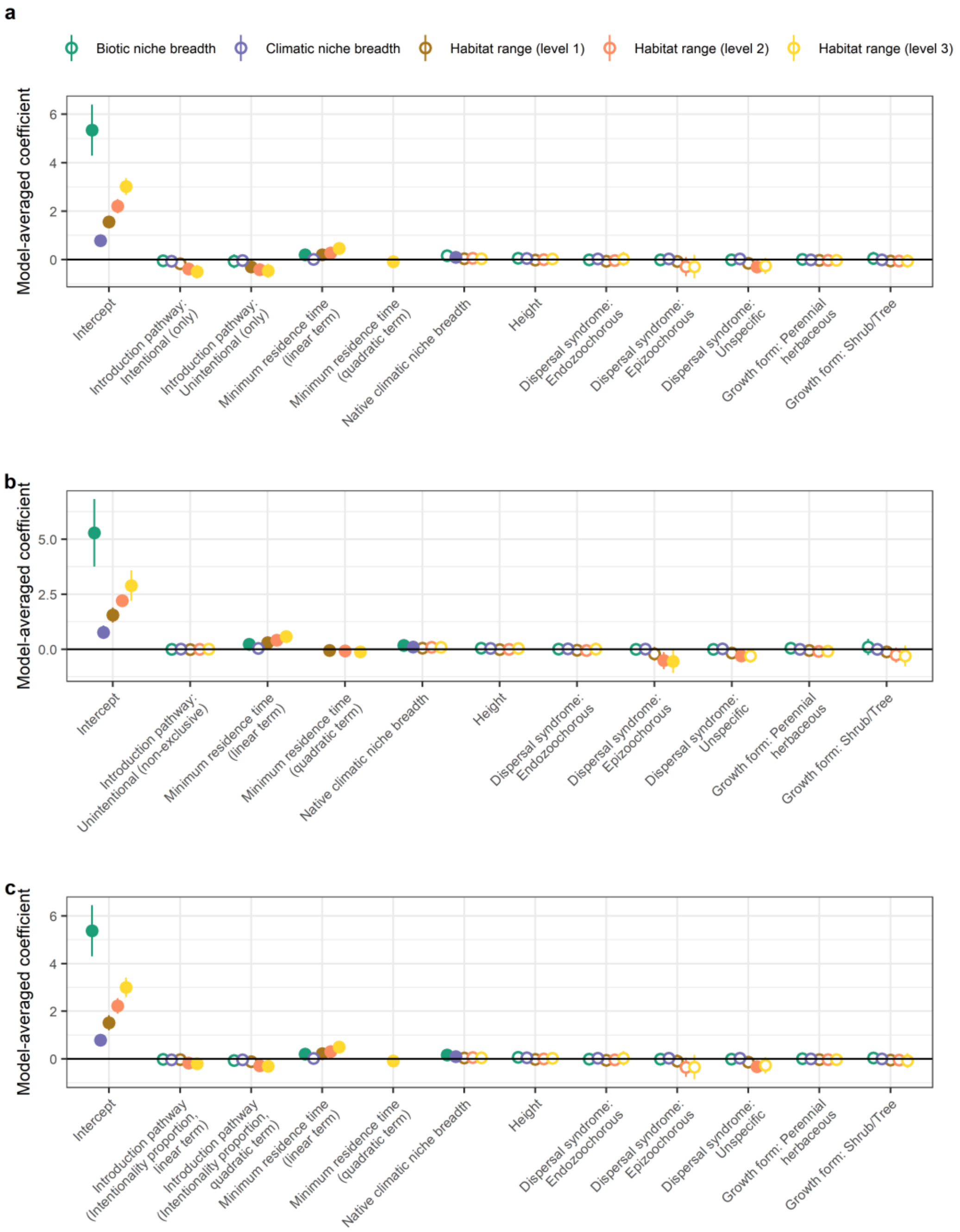


Fig. S3.2. Model-averaged coefficients of introduction pathways, plant traits and minimum residence time on five metrics of niche breadth of non-native plants in Europe, across three codings of introduction pathway. Coefficients were obtained from Phylogenetic Least Square models (PGLS, fitted separately to each metric of niche breadth). Habitat range was ln-transformed for analysis, numerical explanatory variables are scaled to mean = 0 and standard deviation = 1. White filling indicates 95% confidence intervals that overlap 0. The intercept is mean niche breadth of non-native plants for the mean value of numerical explanatory variables, and for the reference categories of: introduction pathway both intentional and unintentional (a) or exclusively intentional (b), dispersal anemochorous (a-c), growth form annual herbaceous (a-c). N = 220 for the habitat range and climatic niche breadth models, N = 215 for the biotic niche breadth model.

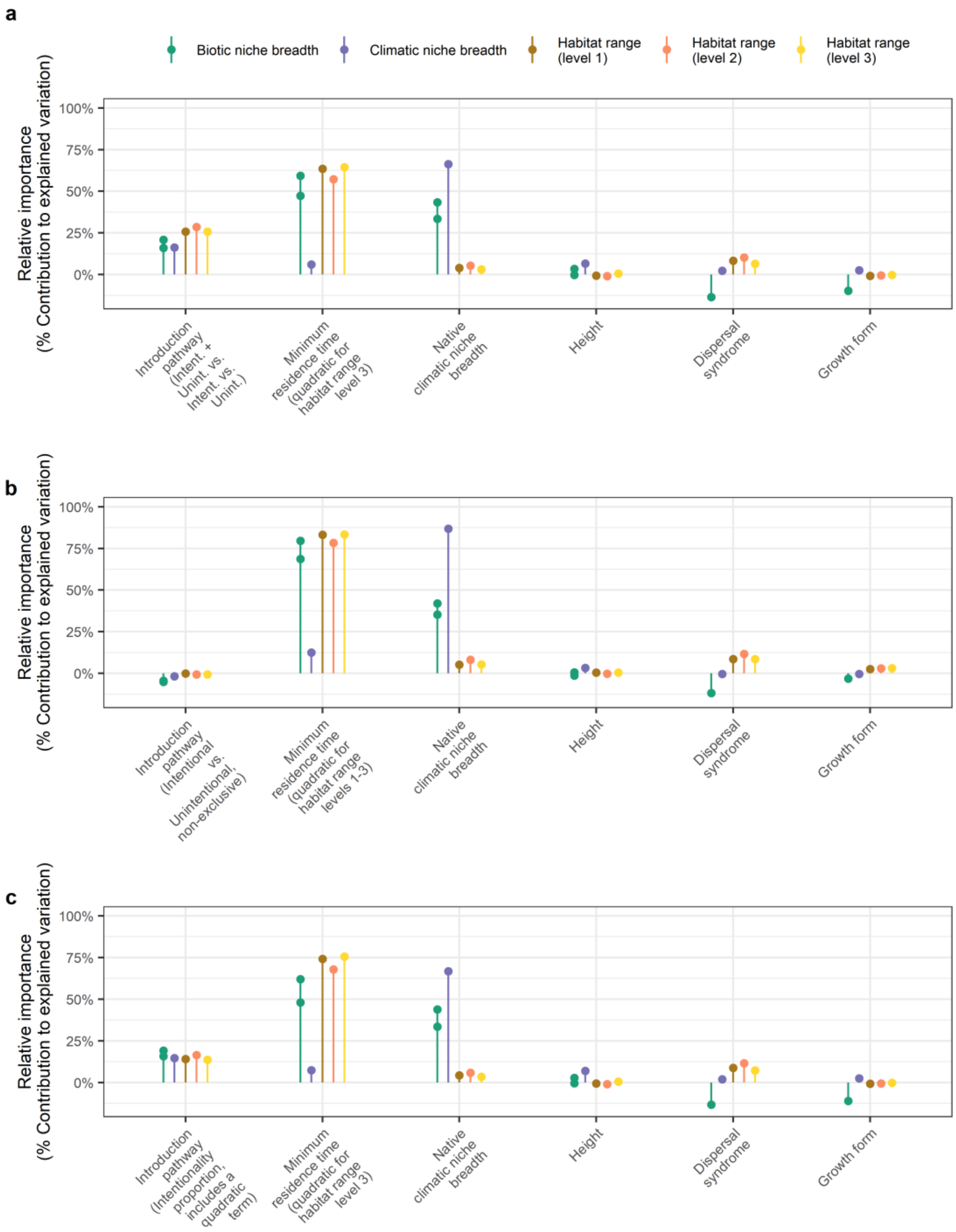
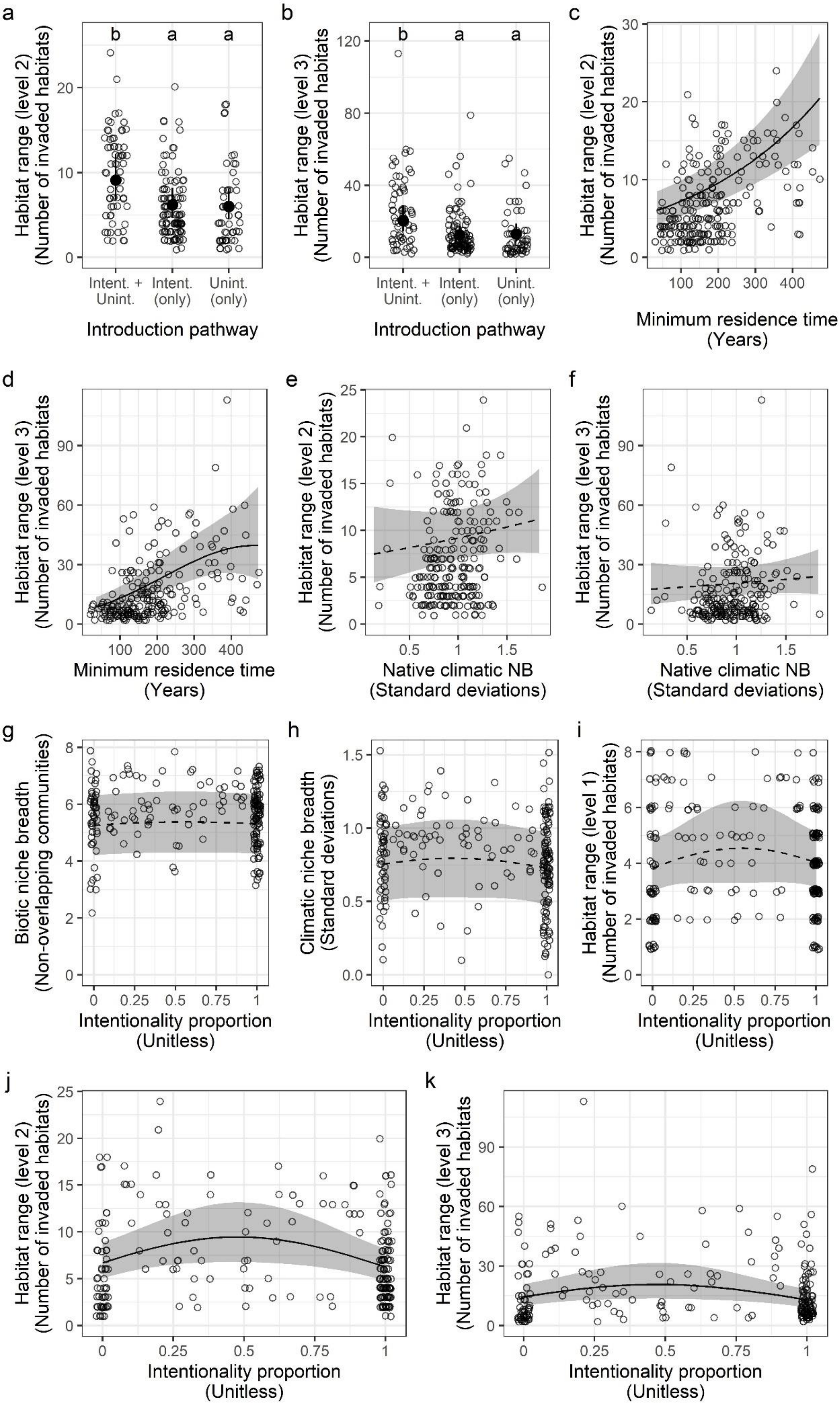
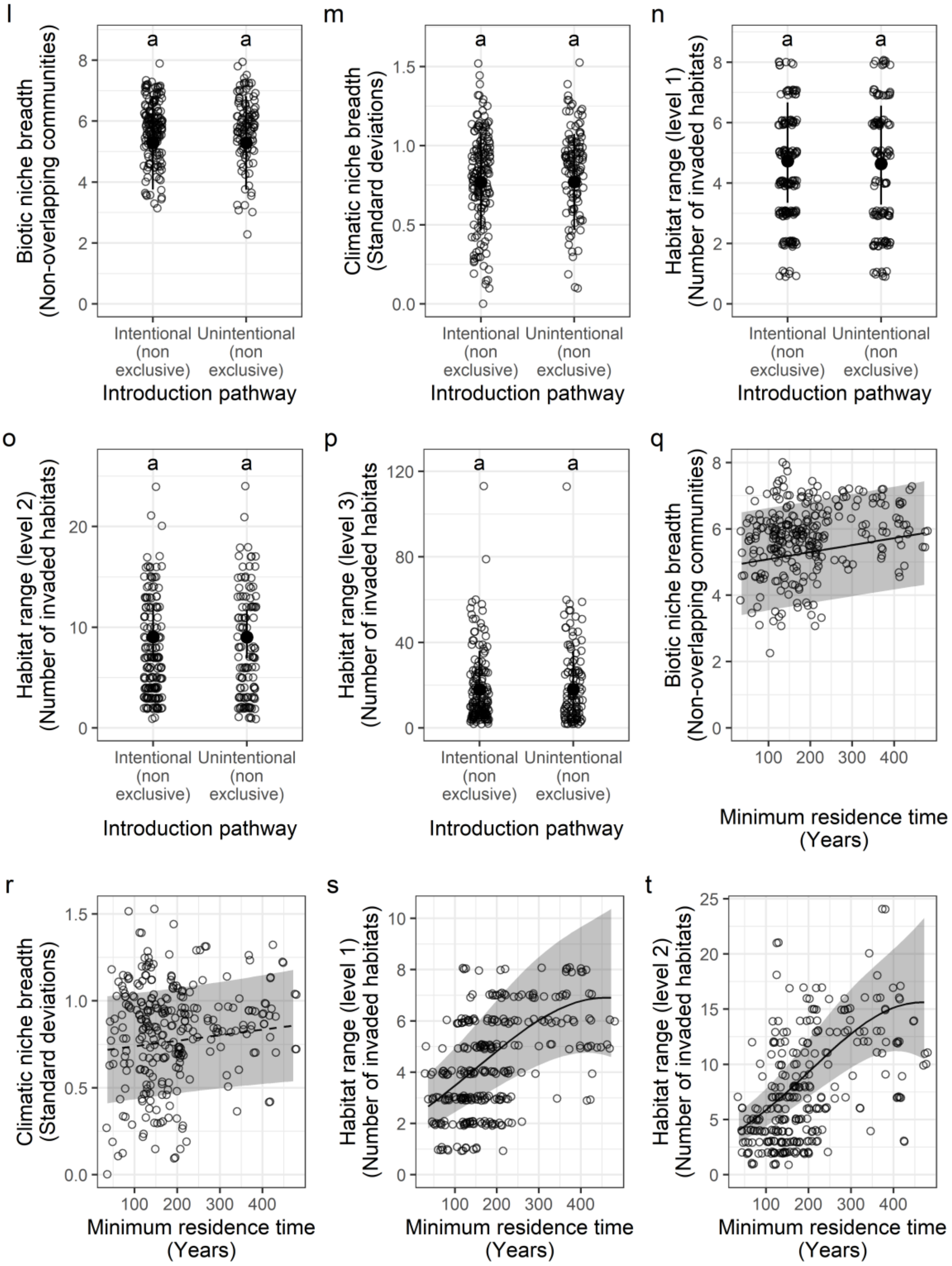


Fig. S3.3. Relative importance of drivers of five metrics of niche breadth of non-native plants in Europe, across three codings of introduction pathway. Relative importance was calculated through dominance analysis, the y-axis shows standardized general dominance. Note that dispersal syndrome and growth form yielded negative values of relative importance in models of biotic niche breadth, and that their removal had little effect on the relative importance of other variables (two dots depict relative importance with and without them). N = 220 for the habitat range and climatic niche breadth models, N = 215 for the biotic niche breadth model.


a
b
c
d
e
f
g
h
i
j
k
Habitat range (level 1) (Number of invaded habitats)
Habitat range (level 2) (Number of invaded habitats)
Habitat range (level 3) (Number of invaded habitats
Biotic niche breadth (Non-overlapping communities)
Climatic niche breadth (Standard deviations)
Intent. + Unint.
Intent. (only)
Unint. (only)
Introduction pathway
Minimum residence time (Years)
Native climatic NB (Standard deviations)
Intentionality proportion (Unitless)


l
m
n
a
a
Biotic niche breadth (Non-overlapping communities)
Climatic niche breadth (Standard deviations)
Habitat range (level 1) (Number of invaded habitats)
Intentional (non exclusive)
Unintentional (non exclusive)
Introduction pathway
0
2
4
6
8
0.0
0.5
1.0
1.5
o
p
q
Habitat range (level 2) (Number of invaded habitats)
Habitat range (level 3) (Number of invaded habitats
0
10
20
40
80
120
Minimum residence time (Years)
100
200
300
400
r
s
t
Climatic niche breadth (Standard deviations)
Habitat range (level 1) (Number of invaded habitats)
Habitat range (level 2) (Number of invaded habitats)
5
15
25

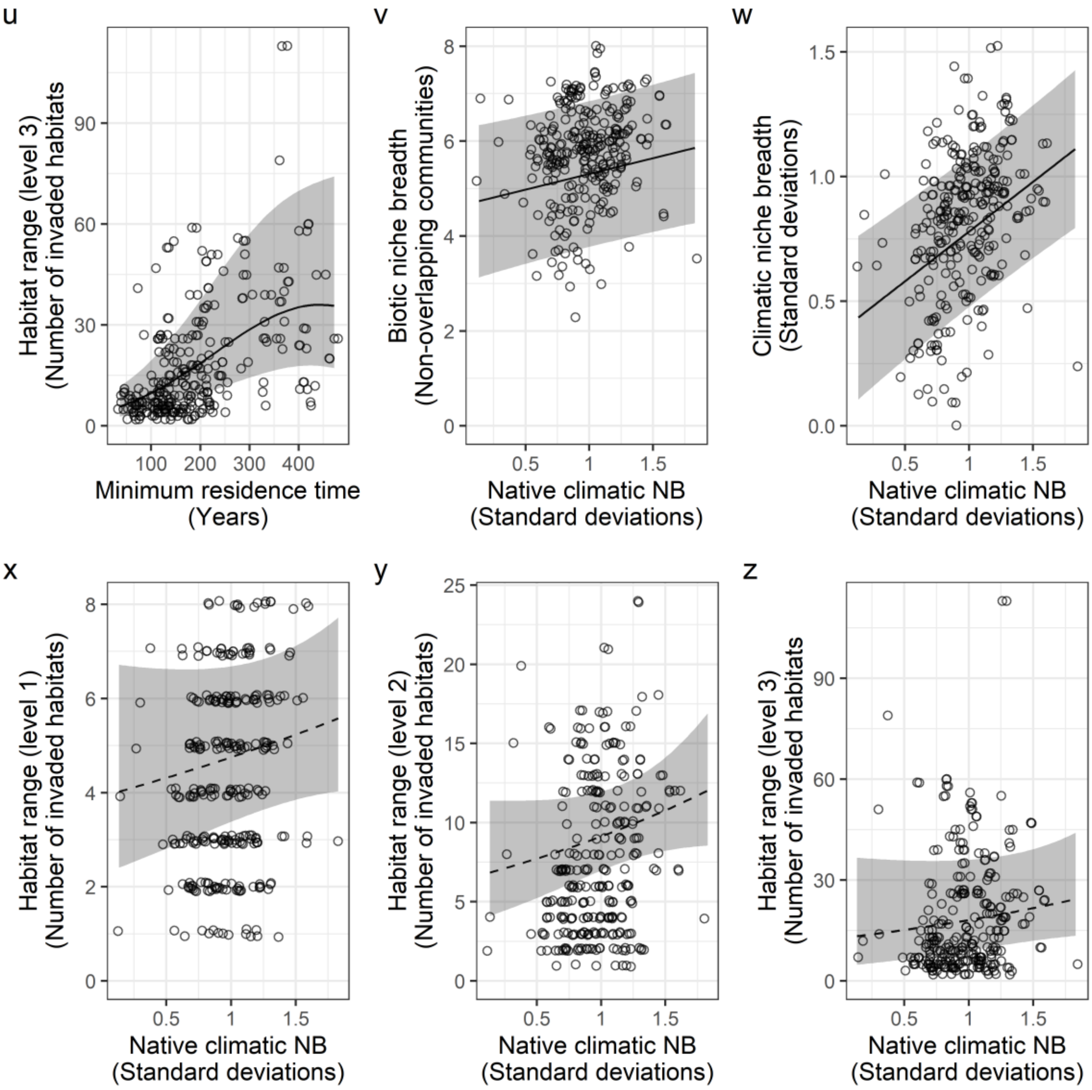


Fig. S3.4. Effect of key drivers on five metrics of niche breadth, using complementary pathway codings: pathway as three categories (a-f), pathways as intentionality proportion (g-k), pathways as two categories (l-z). Model-averaged predicted means (a-b, l-p) and trends (c-k, o-z). Different letters above means indicate statistically significant pairwise differences (Tukey contrast), while dashed lines indicate non-significant slopes), with 95% confidence intervals. Dots show non-native plant species, with random noise added for visualization. Note that habitat range predictions were back-transformed from the log scale. N = 220 (a-f, h-k), N = 215 (g), N = 282 (l, q, v), N = 277 (m-p, r-u, x-z). Abbreviations: Intent. = Intentional, NB = Niche breadth, Unint. = Unintentional.

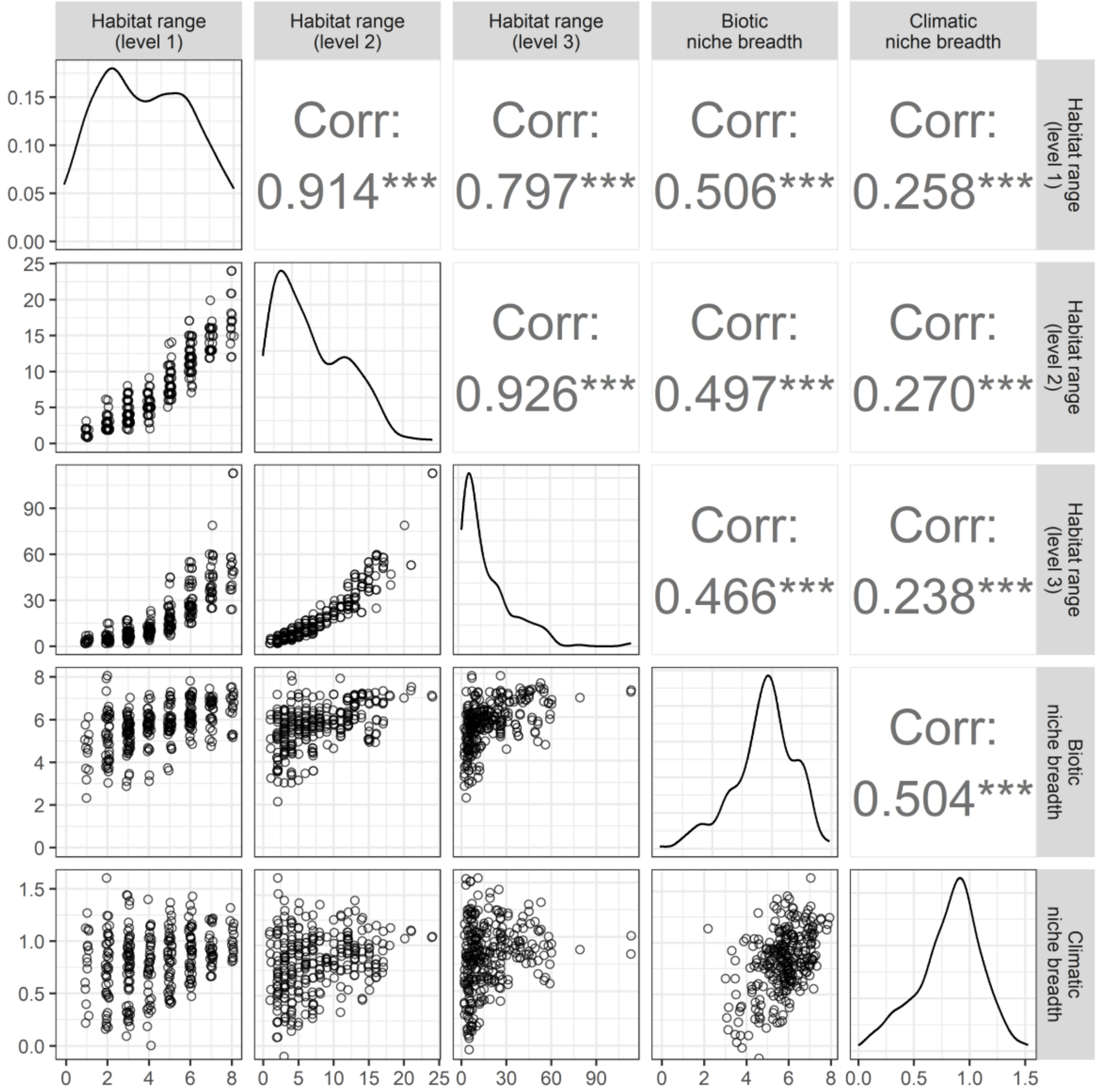


Fig. S3.5. Complementary perspectives of niche breadth are positively correlated, with moderate or weak effect size. Matrix of scatterplots (lower triangle, each dot shows a non-native plant species, with random noise added for visualization.), and Pearson's correlation (upper triangle) among the five metrics of niche breadth. The main diagonal shows a smoothed histogram. N = 220 for correlations not involving biotic niche breadth, N = 215 for correlations involving biotic niche breadth.

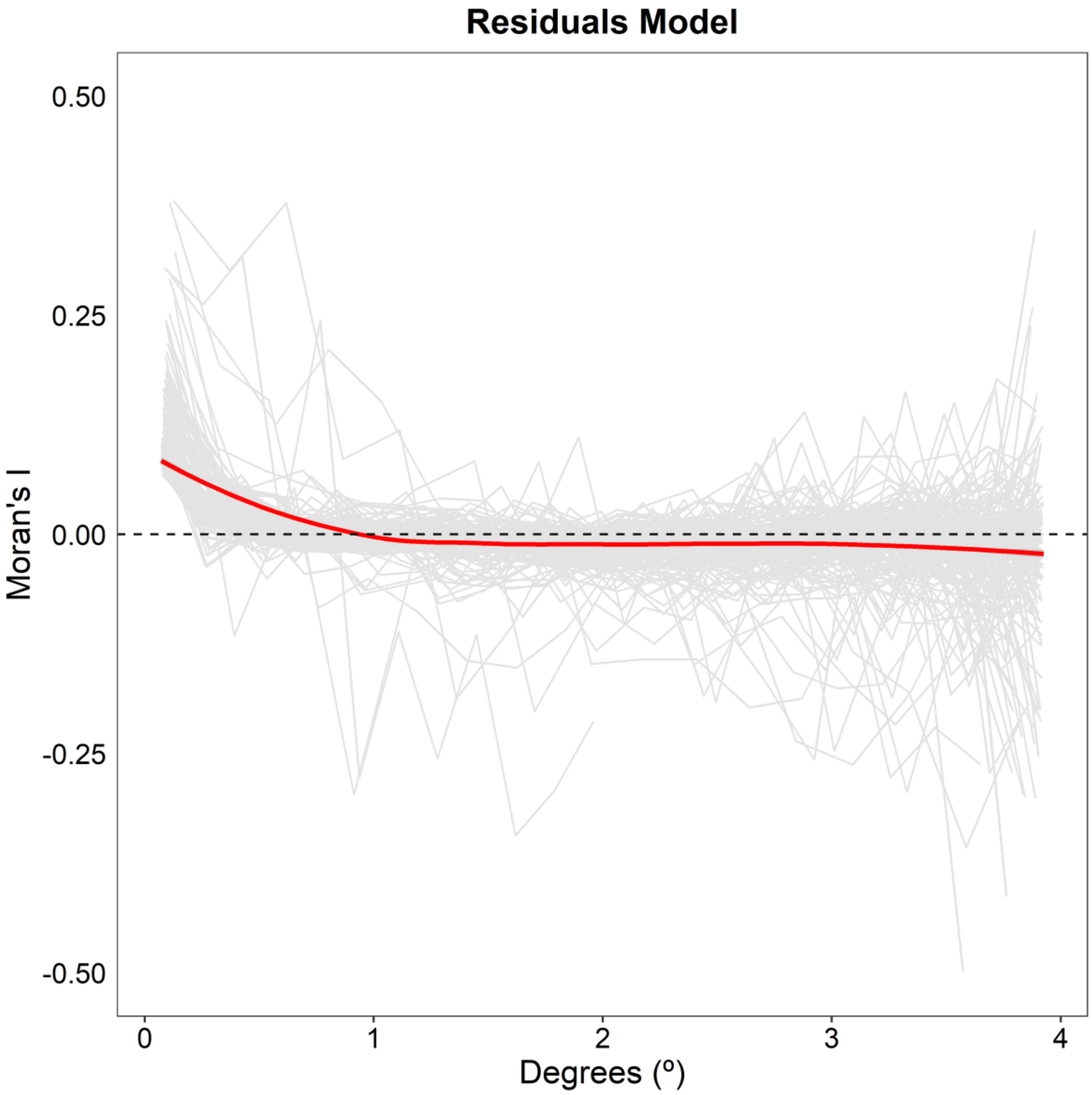


Fig. S3.6. Autocorrelation in model's residuals (N = 200 randomly selected residuals). Correlogram of Moran's I (vertical axis) between residuals separated by a certain distance (horizontal axis, in degrees).

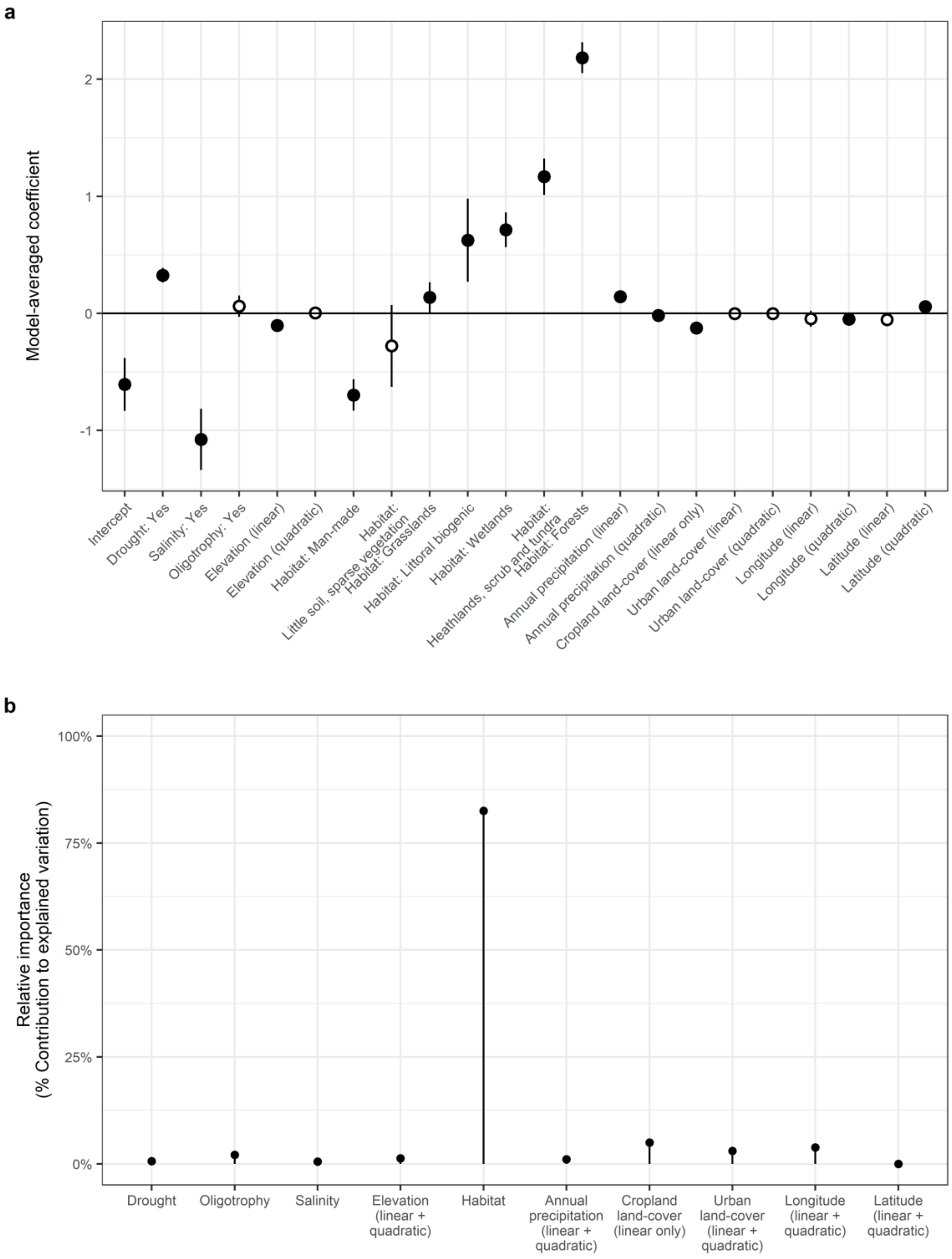


Fig. S3.7. Effects of niche variables on mean intentionality proportion of invaded plots across Europe. Coefficients (a) and relative importance (b), obtained from a Generalized Linear Mixed Model (GLMM), with binomial distribution. Note that numerical covariates are scaled to mean = 0 and standard deviation = 1 (scaling done before fitting quadratic terms). Coefficients are at the logit scale and model-averaged, those with a 95% confidence interval overlapping zero have white filling. The intercept is the mean intentionality proportion for a plot classified to the coastal habitat type, for the mean value of numerical covariates, and that does not endure drought, oligotrophy nor salinity. Relative importance was calculated through dominance analysis, using the marginal R^2 as metric of explained variation (b shows standardized general dominance). N = 61,579 invaded plots. See Fig. 4.2 for a visualization of effects, and Table S3.7 for the numerical values of coefficients and relative importance.

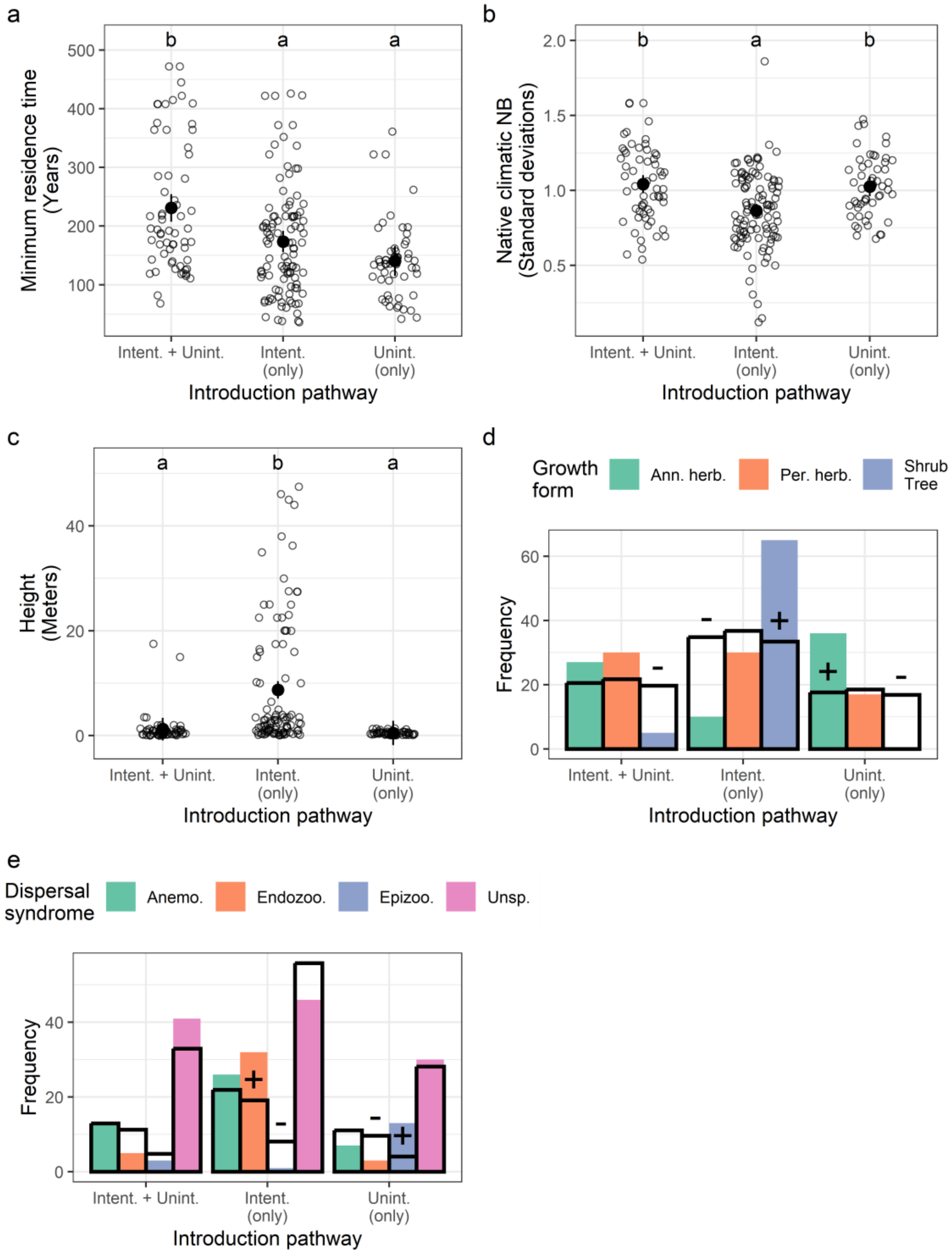
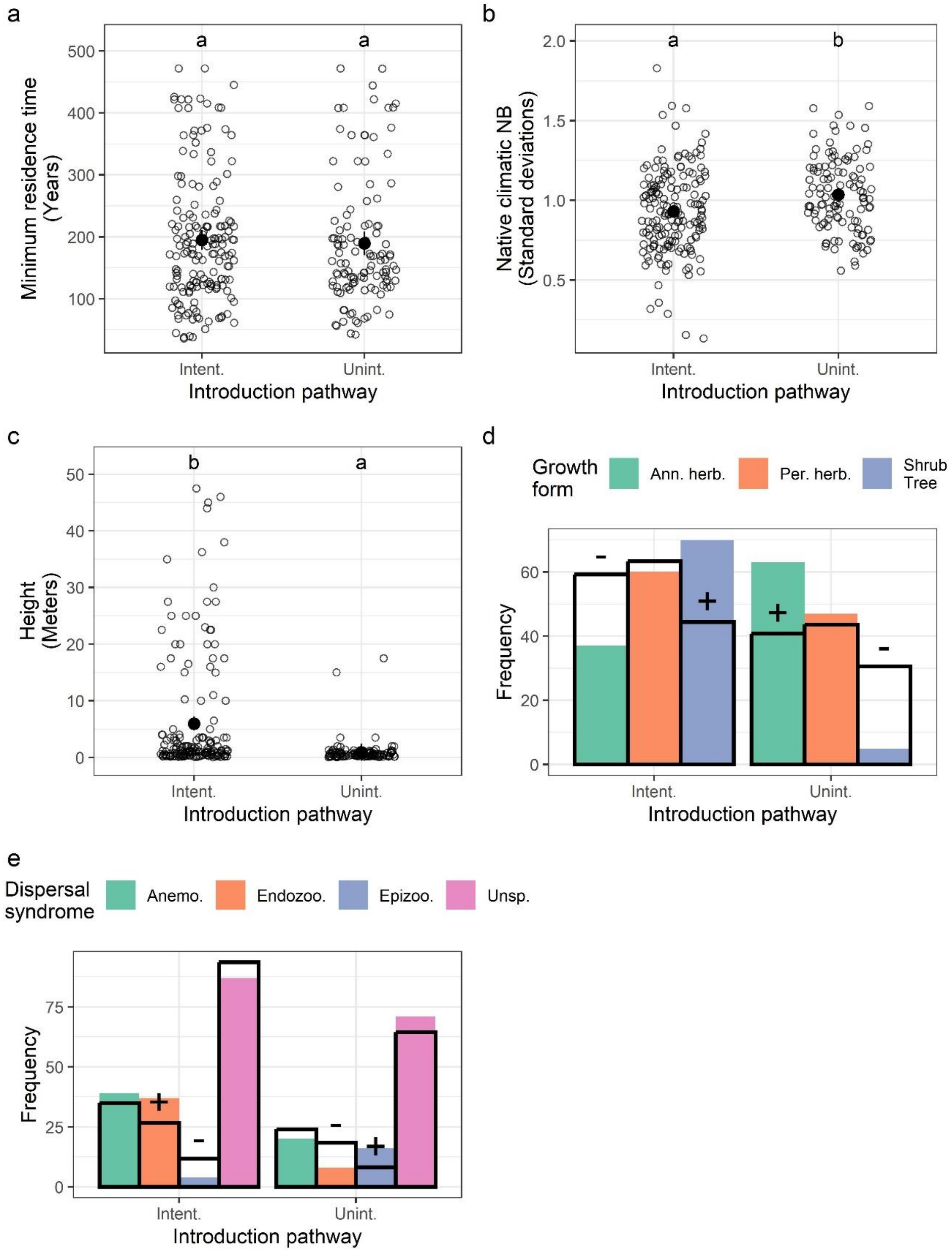


Fig. S3.8. Patterns of covariation between introduction pathway and the characteristics of non-native plants in our dataset. (a-c) Dots show non-native plant species (with random noise added for visualization), while different letters above means indicate statistically significant pairwise differences (Tukey contrast). (d-e) Height of coloured bars shows observed frequencies. Based on a chi-squared test of independence, empty bars show expected frequencies, and plus and minus signs indicate significant greater or less frequency than expected. N = 220 non-native plants. Abbreviations: Anemo. = Anemochorous, Ann. herb. = Annual herbaceous, Endozoo. = Endozoochorous, Epizoo. = Epizoochorous; Intent. = Intentional, NB = Niche breadth, Per. herb. = Perennial herbaceous, Unint. = Unintentional, Unsp. = Unspecific.


a
b
c
d
e
Minimum residence time (Years)
Native climatic NB (Standard deviations)
Height (Meters)
Frequency
Introduction pathway
Intent.
Unint.
a
a
a
b
b
a
500
400
300
200
100
2.0
1.5
1.0
0.5
50
40
30
20
10
0
60
40
20
0
75
50
25
0
Growth form
Ann. herb.
Per. herb.
Shrub Tree
Dispersal syndrome
Anemo.
Endozoo.
Epizoo.
Unsp.
+
-

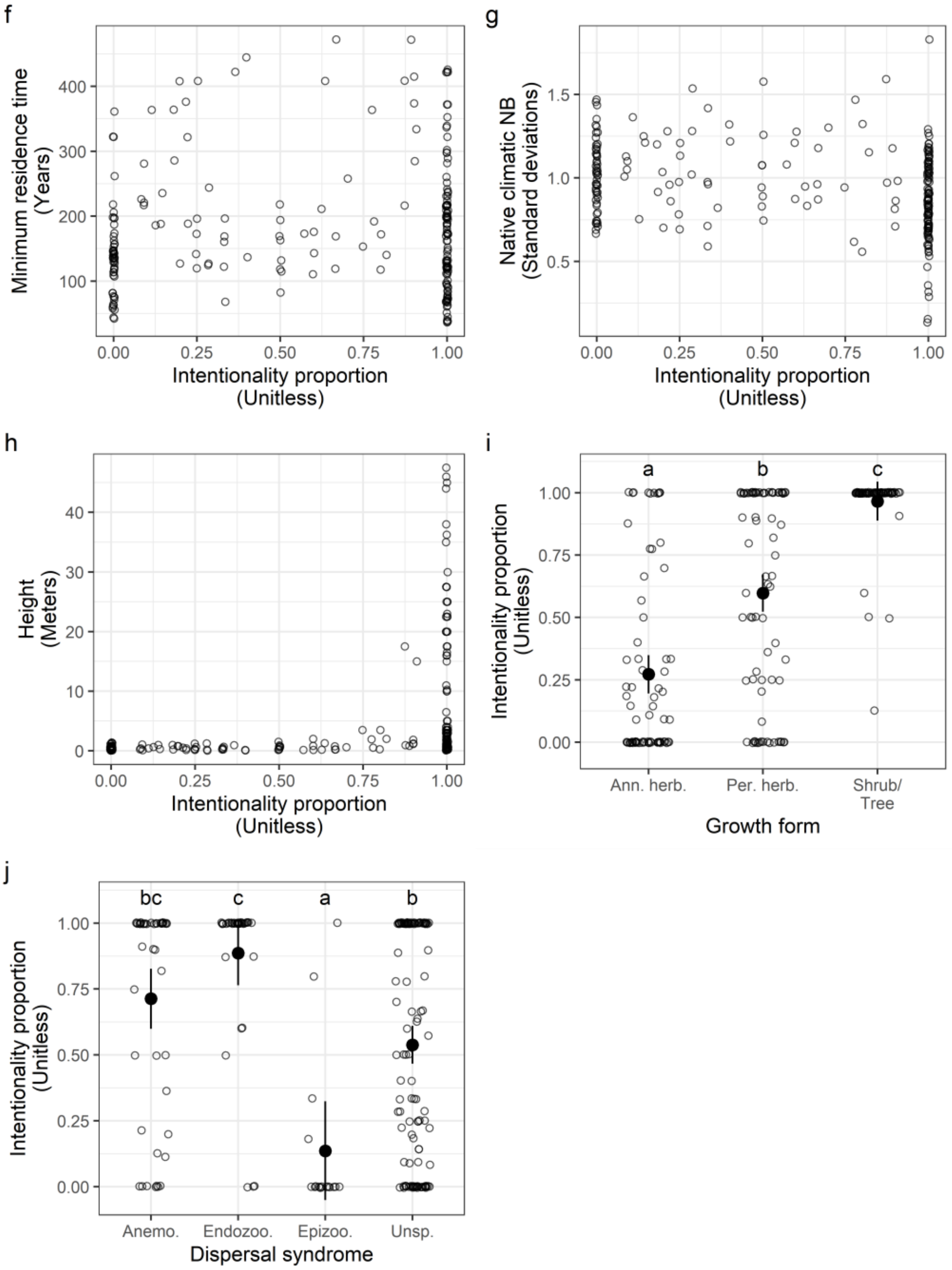


Fig. S3.9. Patterns of covariation between pathways and characteristics of non-native plants, with pathways coded as: (a-e) two categories, and (f-j) intentionality proportion. (a-c, i-j) Different letters above means indicate statistically significant pairwise differences (Tukey contrast). (d-e) Height of coloured bars shows observed frequencies. Based on a chi-squared test of independence, empty bars show expected frequencies, and plus and minus signs indicate significant greater or less frequency than expected. N = 282 non-native plants (a-e), 220 non-native plants (f-j). Abbreviations: Anemo. = Anemochorous, Ann. herb. = Annual herbaceous, Endozoo. = Endozoochorous, Epizoo. = Epizoochorous; Intent. = Intentional, NB = Niche breadth, Per. herb. = Perennial herbaceous, Unint. = Unintentional, Unsp. = Unspecific.

Supplementary results

Introduction pathways vs other niche characteristics.

Annual precipitation was very weakly correlated to reduced invasion by intentional pathways at low and high rainfall values (quadratic convex, peak around 1600 mm, 1% of explained variation). Lastly, geographical position of the plot was associated with small pathway-specific niche differences (4% of explained variation): invasion by intentional pathways was lowest at the Eastern and Western extremes (quadratic convex) and highest at the Northern and Southern edges of the European continent (quadratic concave).

Supplementary discussion

Historical factors (introduction pathways and residence time) played a greater role at determining niche breadth than most of the studied plant characteristics. The only key driver of niche breadth in the invaded range among our studied plant characteristics was the niche breadth in the native range, while plant dispersal syndrome, height, and growth form were of secondary importance. Dispersal syndrome and plant height are important determinants of dispersal distance (Thomson et al., 2011), but are likely insufficient to account for the diversity of dispersal mechanisms used by non-native plants (Fristoe et al., 2021), which would include human-mediated dispersal at the continental scale. Previous insights suggest that dispersal syndrome is not a key driver of niche breadth (Ainsworth & Drake, 2020; Palma et al., 2021), and that the effect of plant height could be heterogeneous and context-dependent (Kinlock et al., 2022). Growth form was largely irrelevant (Giulio et al., 2021), in contrast to other works (Ainsworth & Drake, 2020; Banerjee et al., 2021; Fristoe et al., 2021; Lazzaro et al., 2020). We note that additional processes, such as enemy release (DeWalt et al., 2004), could help non-native plants to overcome environmental barriers, but these lie outside the scope of our paper.

Our results showed that the type of introduction pathways facilitated invasion in concert with habitat type, climate and geography. Forests were mostly invaded through intentional pathways, similarly to North-East Spain (Riera et al., 2024). This could be related to propagule pressure from forestry (Wagner et al., 2017), and greater pre-adaptation to tolerating shade, as this trait is more prevalent among shrubs and trees than herbs (Martin et al., 2009). Intentional pathways promoted invasion with increasing precipitation up to a limit of 1600 mm, possibly because the set of cultivated plants broadens until reaching a point of no shortage in moisture availability. The effect of geographical coordinates probably reflect complex influences of macroclimate and country-specific differences in historical trade and recording of non-native plants (Arianoutsou et al., 2021).

1

Appendix 4

Supplementary Material for Chapter 5

This Appendix contains

Supplementary Methods

Tables S4.1-S4.8

Figures S4.1-S4.5

Supplementary methods

Details on the acquisition and processing of species occurrence data and bioclimatic variables.

We followed the relevant sections of published guidelines (Feng et al., 2019).

(A) Occurrence data

A1) Source of occurrence data

Global Biodiversity Information Facility (GBIF, 2021), with the ‘rgbif’ package (Chamberlain et al., 2021).

A2) Download date; version of data source

19 October 2021

A3) Basis of records

We excluded fossil occurrences and plants in cultivation from our GBiF download (GBIF, 2021), using the ‘rgbif’ package (Chamberlain et al., 2021). After the download, we removed absences with the ‘tidyverse’ package (Wickham et al., 2019).

A4) Spatial extent

For each plant, we quantified niche conservatism between native (global, excluding mainland Spain) and non-native ranges (mainland Spain). Polygons delimiting the native and non-native ranges were taken from the Taxonomic Database Working Group (Brummitt, 2001). We ignore whether our occurrences corresponded to source or sink populations.

A5) Temporal range

We did not perform filtering of occurrences based on year.

A6-1) Duplicate coordinates.

We removed duplicate coordinates from the GBiF download using the ‘tidyverse’ package (Wickham et al., 2019). Moreover, a single pixel of the bioclimatic rasters could contain many occurrences of the same species. We cropped and masked the bioclimatic raster (only the first bioclimatic layer) to the mainland Spain polygon, and extracted bioclimatic data onto the cleaned occurrences with the extract() function (with the argument: cells = TRUE) from the ‘raster’ package (Hijmans, 2021). We removed occurrences without bioclimatic data, and we kept only one occurrence per pixel, with the ‘tidyverse’ package (Wickham et al., 2019).

A6-2) Spatial and environmental outliers, error

We did not address the spatial distribution of points (spatial clustering, disjunct occurrences, etc.), which would be unfeasible given the large sample size, and the lack of independent fine-scale distribution data for comparison. We note that spatial “outliers” (i.e. disjunct spatial patterns of occurrences) are naturally occurring in native (e.g. bore-alpine disjunctions) and non-native ranges (e.g. geographically disjunct introduction epicentres might lead to multiple independent introductions). We think that our dataset prevented at least some of these errors by excluding from our initial download some large citizen-science datasets (iNaturalist, Pl@ntnet). Such datasets may be prone to including mistaken identifications, and plants in cultivation in public or private gardens.

A6-3) Spatial coordinates and uncertainty

We excluded occurrences without coordinates or with geospatial issues from our GBiF download (GBIF, 2021), using the 'rgbif' package (Chamberlain et al., 2021). After the download, we used the 'CoordianteCleaner' package (Zizka et al., 2019) to remove coordinates located in country centroids and biodiversity institutions (2-km buffer), or located in the open sea (buffland polygons). Regarding coordinate uncertainty, we kept coordinates without data on uncertainty, and when such data was provided, we excluded coordinates with more uncertainty than the resolution of the bioclimatic raster, using the 'tidyverse' package (Wickham et al., 2019). Raster resolution changes with latitude, so we calculated the threshold of unacceptable uncertainty (in meters) with the following formula (taken from: https://opendem.info/arc2meters.html): cosinus(LAT * PI / 180) * 1852 * RES; where LAT is the latitude, PI is a constant to convert latitude into radians (π = 3.141593), and RES is the resolution of the raster in arc-minutes (2.5 in our case).

A7-1) Sampling bias

We did not address sampling bias specifically, but we think our procedure of keeping only one coordinate per pixel reduced the impact of sampling bias on our analyses.

A7-2) Spatial autocorrelation

We did not address the spatial distribution of the points (see sections A61-A63 for filtering procedures). We did not address the spatial autocorrelation in bioclimatic variables extracted on those points either (Sillero & Barbosa, 2021).

(B) Environmental data

B1) Source

WorldClim version 1.4 (Hijmans et al., 2005)

B2) Download date; version of data source

WorldClim version 1.4 (Hijmans et al., 2005); downloaded through the getData() function form the 'raster' package (Hijmans, 2021), on 22 October 2021.

B3) Spatial resolution

2.5 arc-minutes (around 4.5 km at the Equator, around 3.5 km in Spain).

B4) Temporal range

1950-2000

Details on accounting for phylogenetic relatedness in the Dirichlet regression

We accounted for phylogenetic relatedness by including phylogenetic covariates: ordination axes representing phylogenetic relationships, obtained from a principal coordinate analysis on a matrix of phylogenetic distances (Desdevises et al., 2003; Lososová et al., 2006). We only included phylogenetic covariates that were significantly related to the response in single-variable models (p-v < 0.05 in a likelihood ratio test), precision was modelled with an intercept for both the single-variable and the null model. We obtained a time-calibrated phylogenetic tree of the non-native plant species in our dataset using the 'V.PhyloMaker' package (Jin & Qian, 2019), which provides a mega phylogeny expanding on previous work (Smith & Brown, 2018; Zanne et al., 2014). The tree was obtained with default settings (nodes = build.nodes.1, scenarios = "S3"), and we bounded genera absent from the tree to a closely related genus.

Supplementary tables

Table S4.1. Overview of previous studies on drivers of niche conservatism of non-native plants (ordered from oldest to newest); focusing on the aspects that we think are most relevant to compare to our study. We note that not all studies used Schoener's D as a matrix of niche overlap. This selection of papers is partly based on the list of references used by a recent metanalysis on niche conservatism (Liu et al., 2020), and was complemented by screening the references on papers on niche conservatism. Abbreviations: ANOVA = Analysis of Variance; E = Expansion; ENM = Environmental Niche Models; GLM = Generalized Linear Model; KS = Kernel Smoothers; LM = Linear Model, MRT = Minimum Residence Time; O = Overlap; PCA = Principal Component Analysis; TPD = Trait Probability Density; U = Unfilling; USA = United States of America.

Reference	N species	Has non-analog climates?	Method	Metrics	Pathway	MRT	Traits	Interact	Method relating niche metrics to plant's attributes	Location native range	Location invaded range
(Gallagher et al., 2010)	26	Yes	PCA	Between-class inertia ratio	No	Yes	Native range size, native biogeographic province, longevity (annual/perennial), growth form (grass, herb, vine, shrub, tree), dispersal, seed mass	No	Non-parametric (Spearman's correlation, Wilcoxon signed-rank test, Kruskal-Wallis)	Anywhere	Australia
(Petitpierre et al., 2012)	50	No	PCA + KS	OUSE	No	Yes	No	No	Not specified	Eurasia and North America	Eurasia and North America
(Early & Sax, 2014)	51	Yes, also models only analog	PCA + KS	E, shift distance, native-naturalized disequilibrium	No	Yes	Range size, niche breadth, marginality, dispersal ability, generation time	MRT x generation time	LM, Quasibinomial GLM (+ multimodel inference)	Europe	Contiguous USA
(Donaldson et al., 2014)	11	Yes	ENMs	O	Ornamental, forestry, dune stabilization	No	No (all were trees: *Acacia* species)	No	None	South-Africa	Australia
(Dellinger et al., 2016)	26 (13 pairs)	Yes, also models only analog	PCA + KS	OUE, position and breadth shift	No	No	Native niche breadth, reproductive mode	No	Linear mixed models (random effect = family)	Anywhere	Anywhere
(Atwater et al., 2018)	815	Yes	PCA + KS	OAUSEP, centroid shift	No cultivation, some cultivation,	No	Growth form (graminoid, forb, subshrub, shrub, tree, vine), life	No	Linear mixed models (random	Anywhere	Anywhere

					wide cultivation		span (annual, biennial, perennial, woody)		effect = taxonomy)		
(Liu et al., 2020)	137 (Fig. 3)	No	Meta-analysis of PCA + KS	USE, similarity, breadth ratio	Intentional (only), unintentional (only), both	Yes	No	No	Bayesian hierarchical models (random effect = study)	Anywhere	Anywhere
(Sychrová et al., 2022)	59	No	PCA + KS	OUE	No	Yes	Native range size, biomes in the native range. All were trees and shrubs	No	Non-parametric (Spearman’s correlation, Kruskal-Wallis)	North America	Europe
(Vásquez-Valderrama et al., 2022)	107	Yes	PCA + KS + TPD	O, dissimilarity, nestedness, climate range size difference	No	No	Leaf area, specific leaf area, leaf nitrogen, plant height, specific stem density, seed mass. All were woody Fabaceae.	No	ANOVA	Anywhere	Anywhere
Our paper	164	Yes	PCA + KS	OAUSEP	Agriculture, forestry, gardening, unintentional	Yes	Growth form (annual herb, perennial herb, shrub/tree), native climatic niche breadth	MRT x pathway, MRT x growth form	Mixed-effects beta regression (random effect = taxonomy), Dirichlet regression (phylogenetic covariates) (+ dominance analysis)	Anywhere	Mainland Spain

Table S4.2. Plants with edited native ranges: the removed regions were not part of the native background climate, nor did they contribute occurrences. We kept in our analysis some plants that were considered as native to Spain by the Plants of the World Online webpage (POWO, 2021), following the more updated checklist of the vascular flora of the Iberian Peninsula (Ramos-Gutiérrez et al., 2021). In some cases, we removed only occurrences and the background climate for mainland Spain, while in others, we removed also the occurrences and climates in the rest of the "Southwestern Europe" level 2 region. We note that the native and exotic ranges of *Solanum linnaeanum* were switched (i.e. the species was considered as native to Europe and non-native in Africa, the opposite of the consensus at the time of writing). N = 23 species.

Plant name	Removed region
Achyranthes aspera var. *sicula* L.	Spain
Aesculus hippocastanum L.	Middle Asia
Allium neapolitanum Cirillo	Spain
Alnus cordata (Loisel.) Duby	Spain
Cenchrus setaceus (Forssk.) Morrone	West Tropical Africa
Crepis bursifolia L.	Southwestern Europe
Crepis bursifolia L.	Northern Africa
Crepis bursifolia L.	Macaronesia
Crepis sancta (L.) Bornm.	Northern Europe
Crepis sancta (L.) Bornm.	Southwestern Europe
Crepis sancta (L.) Bornm.	Middle Europe
Cymbalaria muralis G.Gaertn., B.Mey. & Scherb.	Spain
Cyperus eragrostis Lam.	South-Central Pacific
Delphinium ajacis L.	Southwestern Europe
Elaeagnus angustifolia L.	Eastern Europe
Gamochaeta coarctata (Willd.) Kerguélen	Mexico
Heliotropium curassavicum L.	China
Heliotropium curassavicum L.	Australia
Heliotropium curassavicum L.	North-Central Pacific
Ipomoea indica (Burm.) Merr.	Northern Africa
Ipomoea sagittata Poir.	Southwestern Europe
Ipomoea sagittata Poir.	Southeastern Europe
Ipomoea sagittata Poir.	Northern Africa
Ipomoea sagittata Poir.	Western Asia
Lunaria annua L.	Spain
Onobrychis viciifolia Scop.	Spain
Panicum capillare L.	Northwest European Russia
Panicum dichotomiflorum Michx.	Southern South America
Panicum dichotomiflorum Michx.	Caribbean

Panicum dichotomiflorum Michx.	Western South America
Panicum dichotomiflorum Michx.	Brazil
Panicum dichotomiflorum Michx.	Northern South America
Panicum dichotomiflorum Michx.	Central America
Petasites pyrenaicus (Loefl.) G.López	Spain
Prunus laurocerasus L.	Western Asia
Prunus laurocerasus L.	Caucasus
Prunus laurocerasus L.	Middle Asia
Solanum linnaeanum Hepper & P.-M.L.Jaeger	Southwestern Europe
Stenotaphrum secundatum (Walter) Kuntze	West Tropical Africa
Stenotaphrum secundatum (Walter) Kuntze	West-Central Tropical Africa
Stenotaphrum secundatum (Walter) Kuntze	Northeast Tropical Africa

Table S4.3. Level 2 polygons removed from the definition of background climate: while they were part of the native range according to the Plants of the World Online webpage (POWO, 2021), they lacked GBiF occurrences.

Plant name	Level 2 region removed from the background climate
Abutilon theophrasti Medik.	Mongolia
Elaeagnus angustifolia L.	Mongolia
Euphorbia serpens Kunth	South-Central Pacific

Table S4.4. Pairwise covariation between explanatory variables, assessed through a calculation of effect size and a significance test. Pairs of variables were ranked from greatest to lowest effect size in absolute value (all metrics of effect size had a theoretical range [0-1] in absolute value). As appropriate, we used: Pearson's correlation and t-test for continuous x continuous, Cramér's V and Chi-square for categorical x categorical (Signorell & mult. al., 2022), and R^2 and ANOVA for continuous x categorical. Abbreviations: ANOVA = Analysis of Variance, cat. = categorical, cont. = continuous, Intro. pathway = Introduction pathway, MRT = Minimum Residence Time, Signif. = Significance. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

Variable 1	Variable 2	Effect size metric	Effect size value	Signif. test	Signif. p-v
Growth form	Intro. pathway	Cramér's V	**0.443**	Chi-square	**0.000**
Native climatic niche breadth	Intro. pathway	R^2	**0.153**	ANOVA	**0.000**
Native climatic niche breadth	Growth form	R^2	**0.128**	ANOVA	**0.000**
MRT	Native climatic niche breadth	Pearson's correlation	0.106	t-test	0.162
MRT	Intro. pathway	R^2	**0.076**	ANOVA	**0.003**
MRT	Growth form	R^2	0.030	ANOVA	0.071

Table S4.5. Coefficients of variables driving the other niche conservatism components (Dirichlet regression; Fig. 5.4 in the main text). Coefficients were at the multinomial logit scale, except for precision, which was at the log scale. Niche conservatism components were calculated with climate data up to the 75th quantile. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

Response	Variable	Coefficient	95% confidence interval (lower bound)	95% confidence interval (upper bound)
Stability	Intercept	1.469	0.479	2.459
	Introduction pathway (Forestry)	1.193	-0.082	2.467
	Introduction pathway (Gardening)	0.551	-0.436	1.538
	Introduction pathway (Unintentional)	0.223	-0.782	1.228
	Growth form (Perennial herb)	0.032	-0.370	0.435
	Growth form (Shrub / Tree)	-0.666	-1.169	-0.164
	Minimum residence time	0.418	0.254	0.583
	Native climatic niche breadth	0.050	-0.116	0.215
	Phylogenetic axis #8	0.064	-0.109	0.237
Expansion	Intercept	-1.145	-2.273	-0.016
	Introduction pathway (Forestry)	0.356	-1.144	1.856
	Introduction pathway (Gardening)	0.313	-0.754	1.380
	Introduction pathway (Unintentional)	0.395	-0.740	1.530
	Growth form (Perennial herb)	0.245	-0.277	0.767
	Growth form (Shrub / Tree)	-0.272	-0.924	0.381
	Minimum residence time	0.405	0.199	0.612
	Native climatic niche breadth	-0.455	-0.673	-0.237

Response	Variable	Coefficient	95% confidence interval (lower bound)	95% confidence interval (upper bound)
	Phylogenetic axis #8	-0.295	-0.510	-0.079
Pioneering	Intercept	-1.265	-2.447	-0.083
	Introduction pathway (Forestry)	0.426	-1.134	1.986
	Introduction pathway (Gardening)	0.325	-0.807	1.457
	Introduction pathway (Unintentional)	0.359	-0.837	1.554
	Growth form (Perennial herb)	-0.095	-0.627	0.438
	Growth form (Shrub / Tree)	-0.403	-1.073	0.267
	Minimum residence time	0.299	0.086	0.512
	Native climatic niche breadth	-0.431	-0.656	-0.207
	Phylogenetic axis #8	-0.171	-0.383	0.042
Precision	Intercept	1.858	1.077	2.640
	Introduction pathway (Forestry)	0.508	-0.622	1.637
	Introduction pathway (Gardening)	0.196	-0.578	0.971
	Introduction pathway (Unintentional)	-0.196	-0.999	0.607
	Growth form (Perennial herb)	-0.040	-0.418	0.339
	Growth form (Shrub / Tree)	-0.247	-0.726	0.232
	Minimum residence time	0.058	-0.102	0.218
	Native climatic niche breadth	0.304	0.156	0.453
	Phylogenetic axis #8	0.149	0.003	0.296

Table S4.6. Effect of quadratic terms on the Akaike Information Crtierion corrected for small sample sizes (AICc), across three levels of removal of marginal climates, in: (a) models of niche overlap (mixed-effects beta regression), (b) models of the other niche conservatism components (Dirichlet regression). Variables were standardized (mean = 0, standard deviation = 1) before fitting the models. Dirichlet regression was implemented following the "alternative" parametrization, where precision was modelled with five explanatory variables (introduction pathway, growth form, minimum residence time, native climatic niche breadth, phylogenetic axis #8). N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

(a) Models of niche overlap (mixed-effects beta regression)

Quantile	Variable	AICc (linear)	AICc (linear + quadratic)	ΔAICC (quadratic & linear – linear)
100% quantile	Minimum residence time	-170.553	-168.791	1.762
	Native climatic niche breadth	-182.386	-182.048	0.338
90% quantile	Minimum residence time	-175.307	-173.508	1.799
	Native climatic niche breadth	-187.485	-187.114	0.370
75% quantile	Minimum residence time	-186.498	-184.683	1.815
	Native climatic niche breadth	-198.967	-198.539	0.427

(b) Models of the other niche conservatism components (Dirichlet regression)

Quantile	Variable	AICc (linear)	AICc (linear + quadratic)	ΔAICC (quadratic & linear – linear)
100% quantile	Minimum residence time	-2,180.304	-2,175.354	4.950
	Native climatic niche breadth	-2,197.355	-2,190.817	6.538
	Phylogenetic axis #8	-2,177.316	-2,173.976	3.340
90% quantile	Minimum residence time	-2,187.244	-2,182.374	4.870
	Native climatic niche breadth	-2,200.131	-2,193.565	6.566
	Phylogenetic axis #8	-2,182.530	-2,179.368	3.162
75% quantile	Minimum residence time	-2,209.071	-2,203.982	5.089
	Native climatic niche breadth	-2,223.474	-2,217.122	6.352
	Phylogenetic axis #8	-2,204.688	-2,202.745	1.943

Table S4.7. Coefficients of correlates of niche overlap (mixed-effects beta regression, genus nested within family; Fig. 5.3 in the main text). Coefficients were at the logit scale. The intercept is the mean niche overlap of plant species for the mean value of numerical covariates, and for the reference categories of annual growth form, and agricultural introduction pathway. Niche overlap was calculated with climate data up to the 75th quantile. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

Variable	Coefficient	95% confidence interval (lower bound)	95% confidence interval (upper bound)
Intercept	-1.075	-1.820	-0.329
Introduction pathway (Forestry)	0.452	-0.516	1.421
Introduction pathway (Gardening)	0.023	-0.676	0.722
Introduction pathway (Unintentional)	0.003	-0.719	0.724
Growth form (Perennial herb)	-0.088	-0.456	0.281
Growth form (Shrub / Tree)	-0.511	-0.957	-0.064
Minimum residence time	0.087	-0.042	0.217
Native climatic niche breadth	-0.275	-0.410	-0.140

Table S4.8. Effect of adding interactions to models containing only additive effects, on the Akaike Information Criterion corrected for small sample sizes (AICc) and a metric of model quality ($R^2_{marginal}$ or pseudo-R^2,as appropriate). (a) models of niche overlap (mixed-effects beta regression), (b) models of the other niche conservatism components (Dirichlet regression). This was done across three levels of removal of marginal climates. Abbreviations: AICc = Akaike Information Criterion corrected for small sample sizes, MRT = Minimum Residence Time, Path. = Introduction pathway. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

(a) Models of niche overlap (mixed-effects beta regression)

Quantile	AICc (additive)	AICc (Path. x MRT)	AICc (Growth form x MRT)	$R^2_{marginal}$ (additive)	$R^2_{marginal}$ (Path. x MRT)	$R^2_{marginal}$ (Growth form x MRT)
100% quantile	-178.311	-173.263	-174.052	0.177	0.189	0.165
90% quantile	-183.537	-178.452	-179.126	0.178	0.190	0.167
75% quantile	-195.379	-190.062	-191.279	0.180	0.190	0.183

(b) Models of the other niche conservatism components (Dirichlet regression)

Quantile	AICc (additive)	AICc (Path. x MRT)	AICc (Growth form x MRT)	pseudo-R^2 (additive)	pseudo-R^2 (Path. x MRT)	pseudo-R^2 (Growth form x MRT)
100% quantile	-2,205.892	-2,173.575	-2,191.130	0.214	0.226	0.230
90% quantile	-2,210.271	-2,176.800	-2,195.137	0.220	0.231	0.235
75% quantile	-2,229.550	-2,194.345	-2,213.760	0.219	0.231	0.236

Supplementary figures

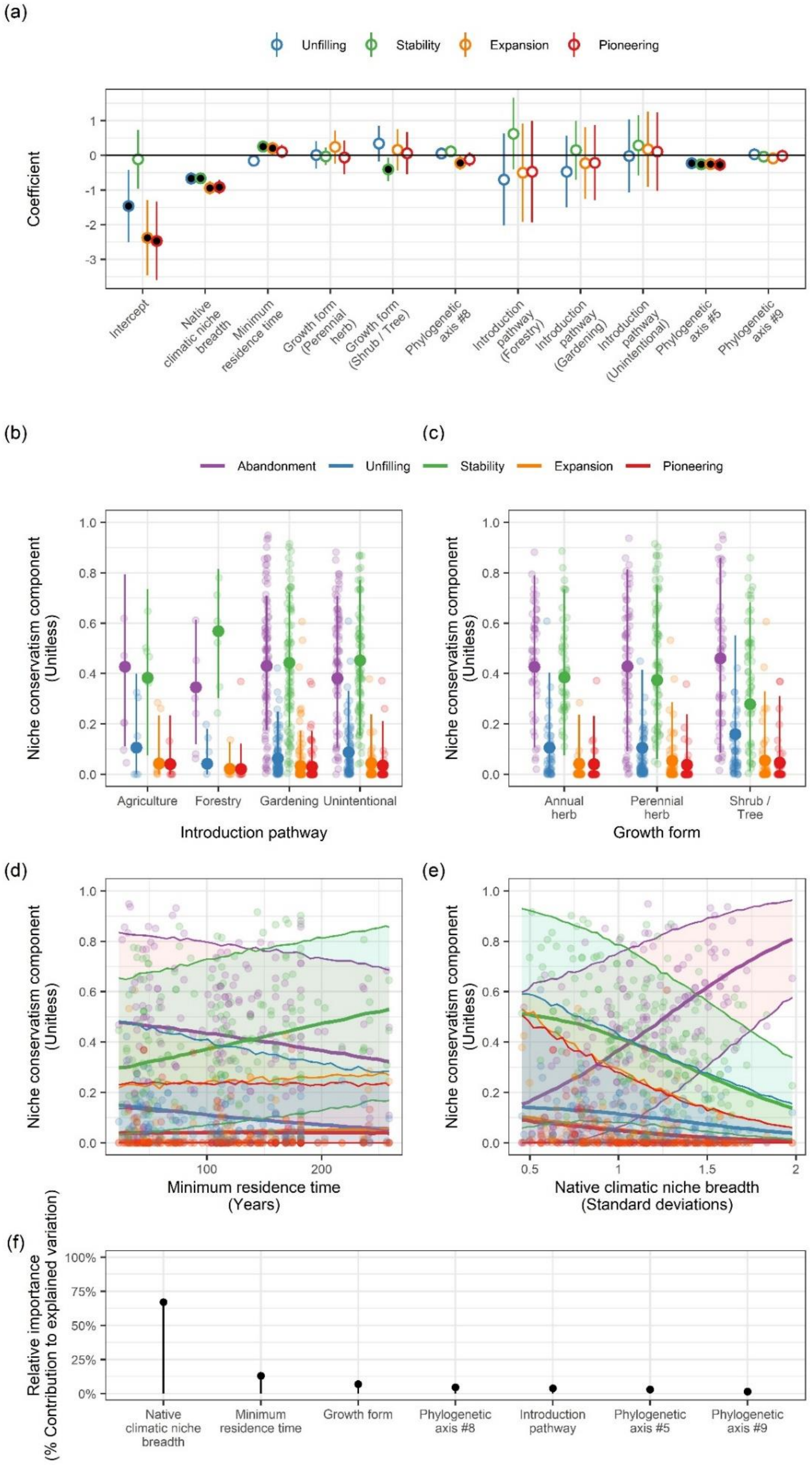
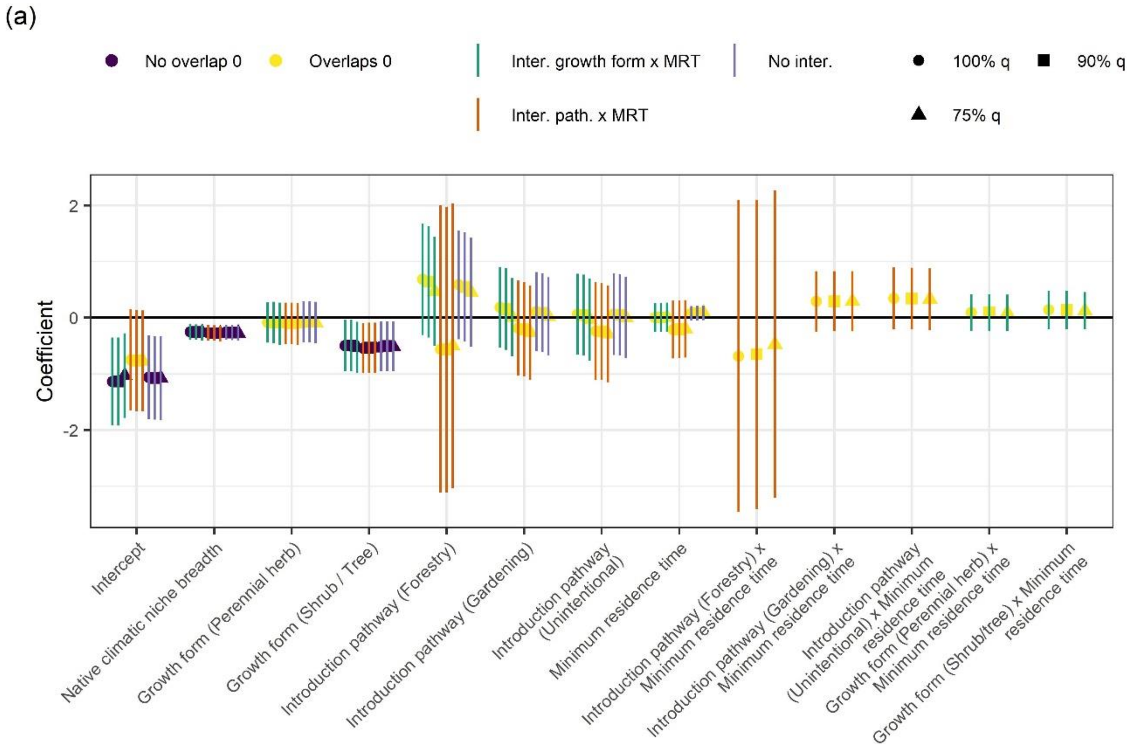


Fig. S4.1. Correlates of niche conservatism components, including abandonment, as modelled by a Dirichlet regression, using data up to the 75th quantile. Abandonment is the base category. This model yielded similar conclusions as the one in the main text, regarding quadratic terms (not supported), interactions (not supported), marginal climates (only 10% of coefficients changed in significance), and effects and relative importance of correlates. In this model, three phylogenetic axes were significant (#5, #8, #9). It has pseudo-R^2 = 0.286. We note than in panel (e), there is a 12% increase in the ratio of (stability)/(unfilling + stability + expansion + pioneering) between species with the narrowest and widest native climatic niche (63% to 75%, model's predictions). (a) Coefficients at the multinomial logit scale, those that included zero in their 95% confidence intervals have white filling. The intercept is the mean niche conservatism component of plants with the mean value of numerical covariates, and the reference categories of annual growth form, and agricultural introduction pathway. (b-e) Predicted niche conservatism components, which always sum up to one for each factor level (b-c), and each value of the numerical covariates. Confidence bands around predicted trends (thick line) are 95% prediction intervals obtained through simulation (Douma & Weedon, 2019) To aid visualization, dots depict non-native plant species with added transparency and random noise (four dots per species), and in panels (b-c), niche conservatism components are plotted side-by-side for each factor level. (f) Relative importance of explanatory variables (% contribution to the total pseudoR^2). N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).


(a)
No overlap 0
Overlaps 0
Inter. growth form x MRT
Inter. path. x MRT
No inter.
100% q
90% q
75% q
Coefficient
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0
-2
Intercept
Native climatic niche breadth
Growth form (Perennial herb)
Growth form (Shrub / Tree)
Introduction pathway (Forestry)
Introduction pathway (Gardening)
Introduction pathway (Unintentional)
Minimum residence time
Introduction pathway (Forestry) x Minimum residence time
Introduction pathway (Gardening) x Minimum residence time
Introduction pathway (Unintentional) x Minimum residence time
Growth form (Perennial herb) x Minimum residence time
Growth form (Shrub/tree) x Minimum residence time

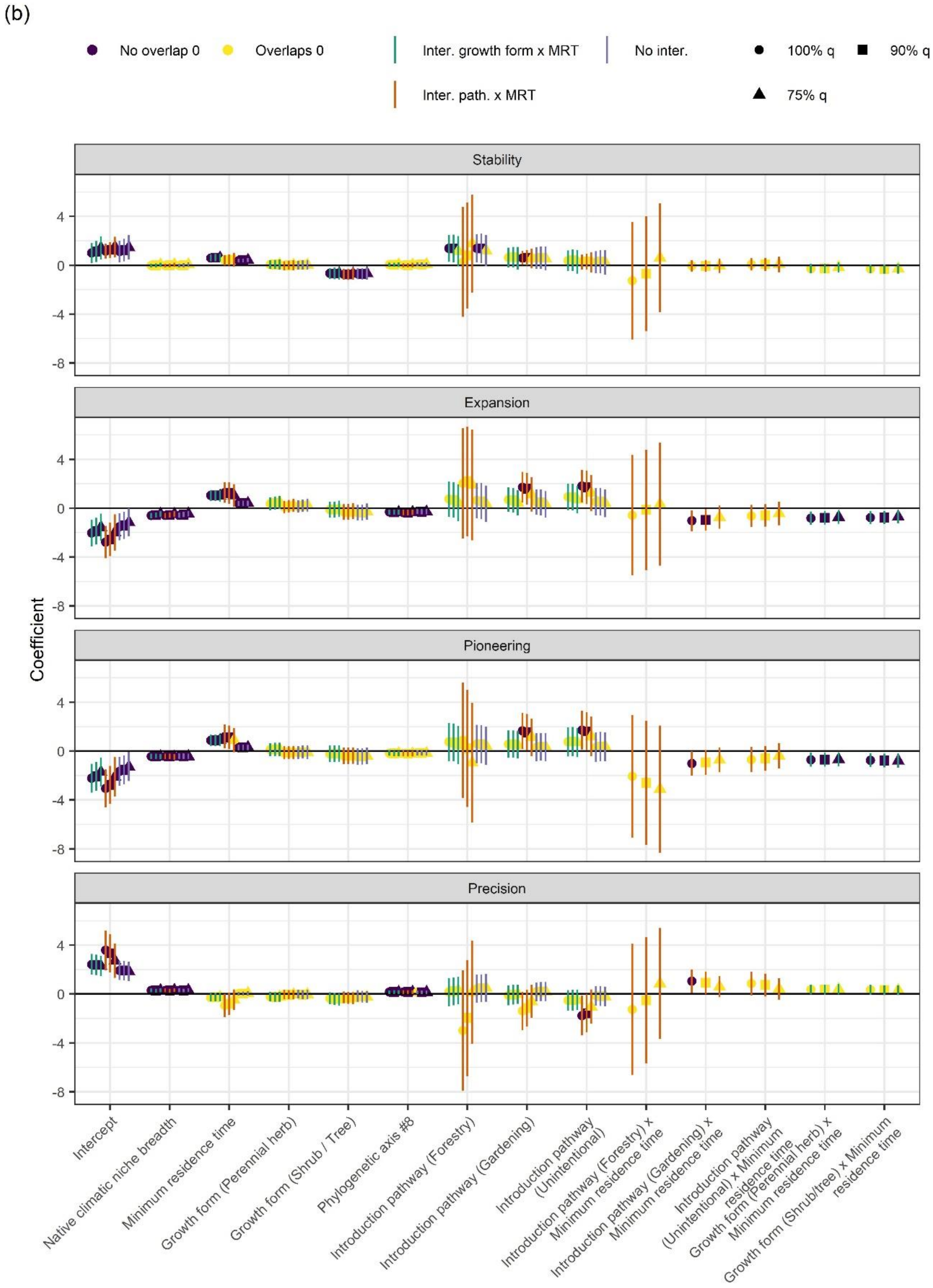


Fig. S4.2. Coefficient across removal of marginal climates (3 shapes), and modelling of interactions (3 colours of vertical bars, which represent 95% confidence intervals), for models of: (a) niche overlap (logit scale, mixed-effects beta regression), (b) other niche conservatism components (Dirichlet regression, expected proportions have coefficients at the multinomial logit scale, while precision was at the log scale). Coefficients that include zero in their 95% confidence interval (vertical bars) are coloured yellow. The intercept is the mean value of plants for the mean value of numerical covariates, and for the reference categories of annual growth form, and agricultural introduction pathway. The main text show the coefficients when no interactions are modelled, with climatic data up to the 75th quantile (Fig. 5.3 for niche overlap, Fig. 5.4 for the other niche conservatism components, except for Precision). No coefficient changed in significance in the models of niche overlap (0 out of 29 combinations coefficient x interactions), while only 10% changed significance in models of the other climatic niche conservatism components (13 out of 128 combinations coefficient x interactions, not taking precision into account). Abbreviations: Inter. = Interaction, MRT = Minimum Residence Time, path. = Introduction pathway, q = quantile. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

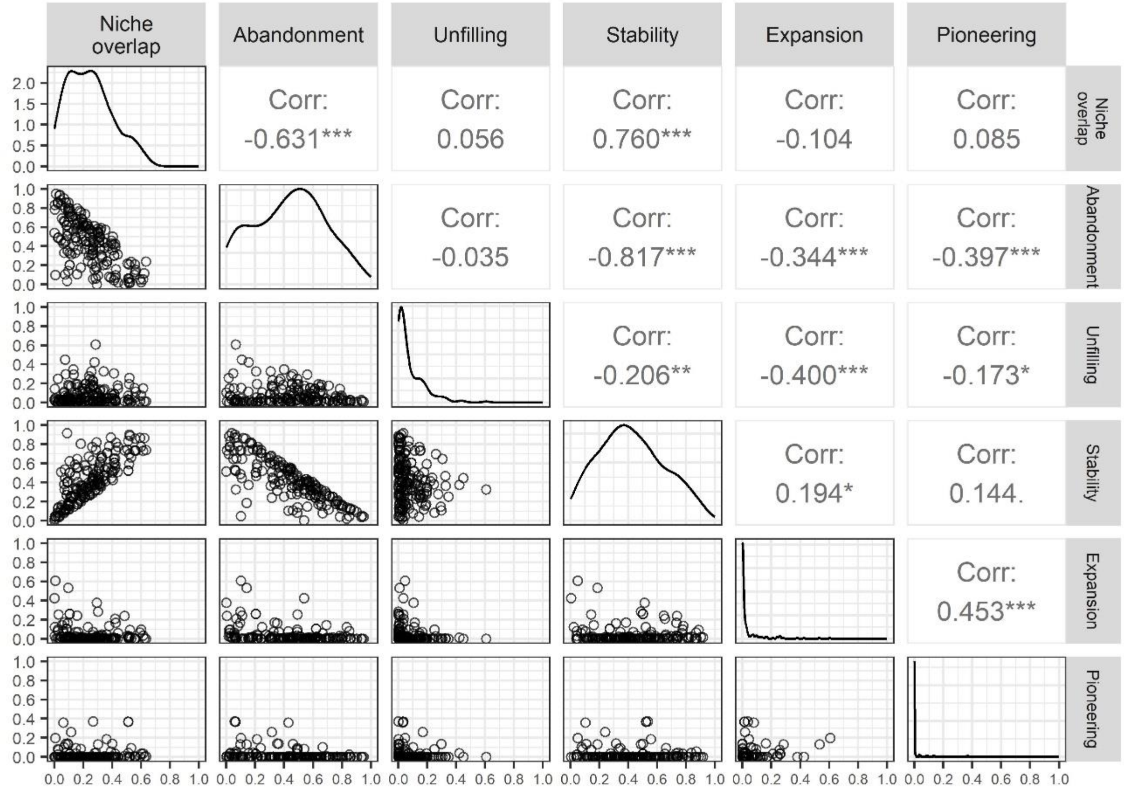


Fig. S4.3. Correlation among the niche conservatism components, including abandonment: scatterplots (lower triangle, with added transparency for visualization), and Spearman's correlation (upper triangle). The main diagonal showed smoothed histograms. All plots used climate data up to the 75th quantile. Significance level of correlations: *** = p-v < 0.001, ** = p-v < 0.01, * = p-v < 0.05, · = p-v < 0.10. N = 175 (164 plants. 11 duplicated since they were introduced through two pathways).

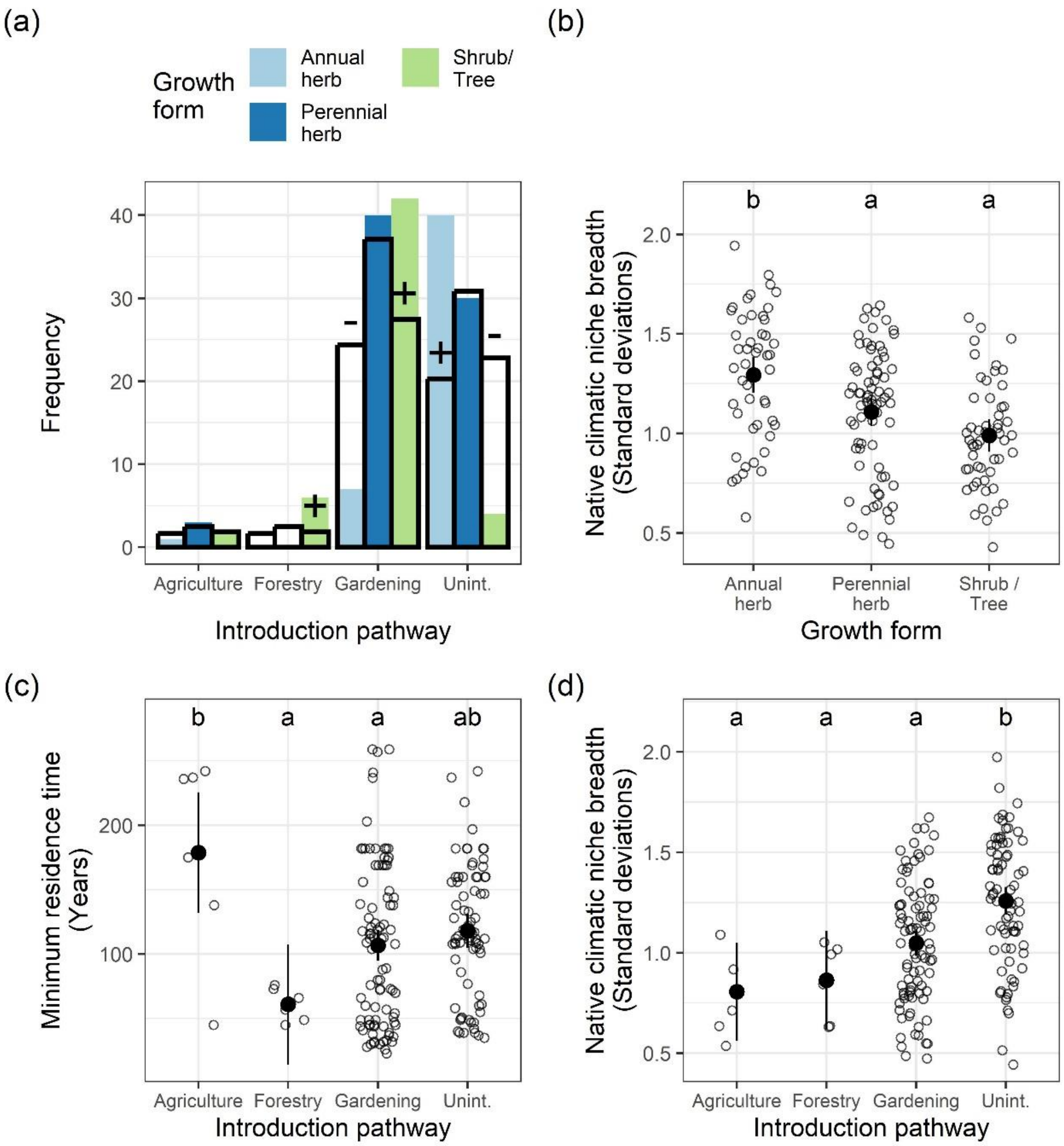
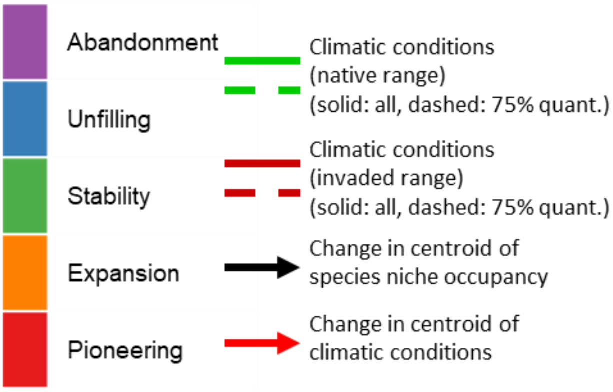
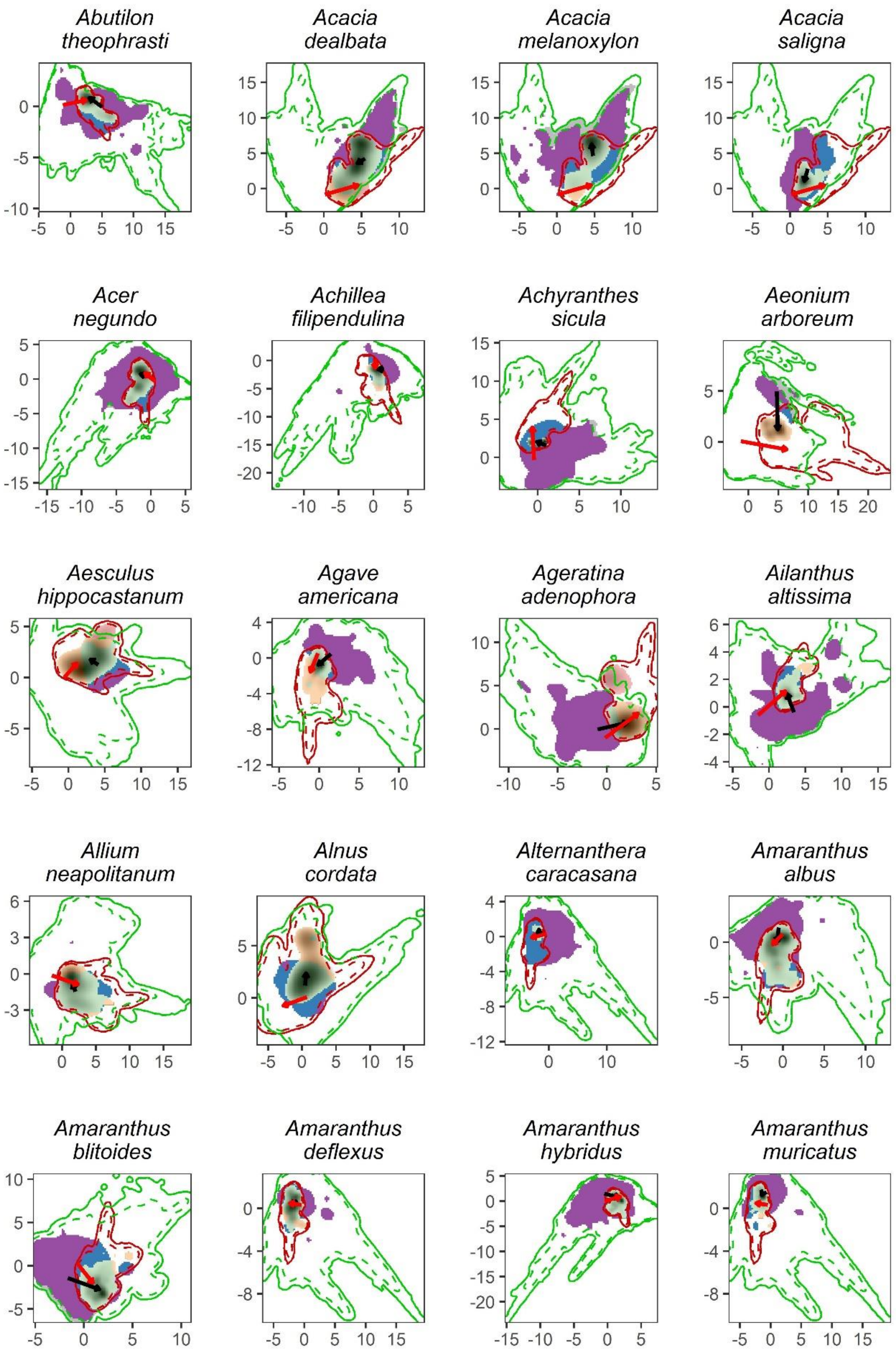


Fig. S4.4. Covariation between explanatory variables (only those significant among all pairwise tests; see Table S4.4). (a) Height of coloured bars shows observed frequencies. Based on a chi-square test of independence, empty bars show expected frequencies, and plus and minus signs indicate greater or less frequency than expected (residual > 1.96 or residual < -1.96, respectively). (b-d) Dots show non-native plant species (with random noise added for visualization), while different letters above estimated marginal means indicate statistically significant pairwise differences (Tukey contrast). N = 175 (164 plants. 11 duplicated since they were introduced through two pathways). Abbreviations: Unint. = Unintentional.

Fig. S4.5. Climatic niches of plant species between the native and invaded ranges, in reduced ordination space (PCA axes), showing only extreme values of metrics of niche conservatism. Except for niche overlap (a) and stability (e), the rest of lowest values excluded zero (c, g, i). Darker shading indicates greater niche occupancy in the invaded range, while grey colour indicates climatic conditions removed from the calculation of niche conservatism metrics, because of their marginality. See Fig. S4.5 for the climatic niches of all species. Abbreviations: quant. = quantile.

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Aeonium arboreum
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Aesculus hippocastanum
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Agave americana
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Ageratina adenophora
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Alternanthera caracasana
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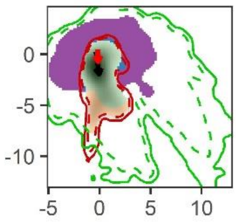
Amaranthus powellii



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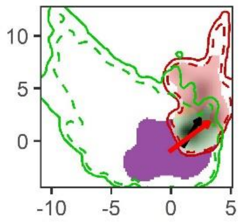

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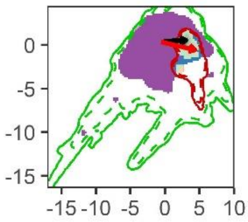

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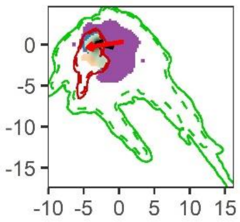

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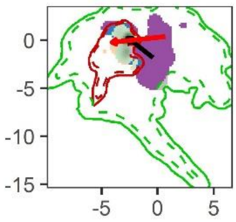
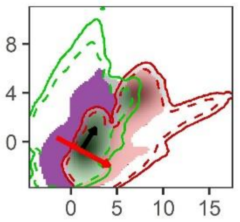
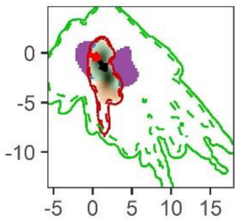


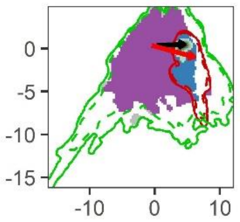
Arctotheca calendula



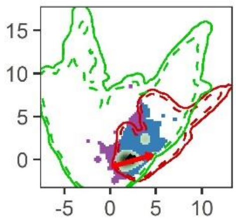
Artemisia verlotiorum



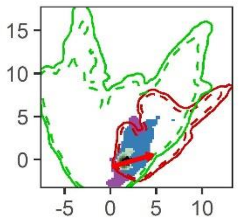
Asclepias curassavica



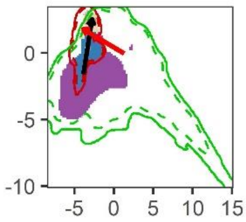
Atriplex semibaccata



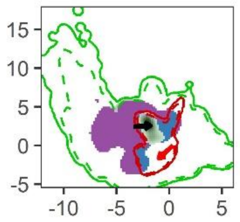
Atriplex suberecta



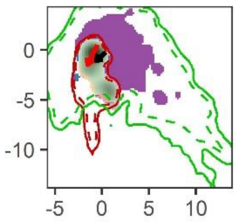
Austrocylindropunti subulata



Baccharis halimifolia



Bidens aurea



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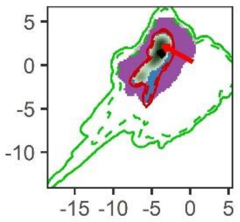
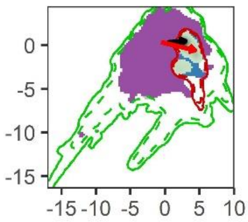


Bidens pilosa



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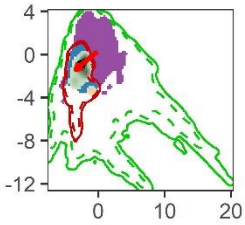

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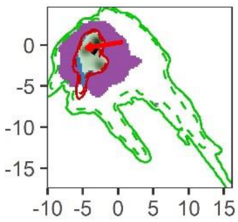

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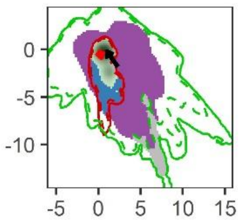
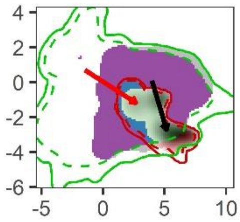


Buddleja davidii



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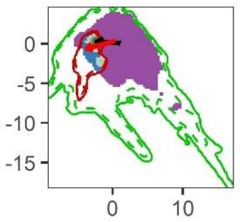

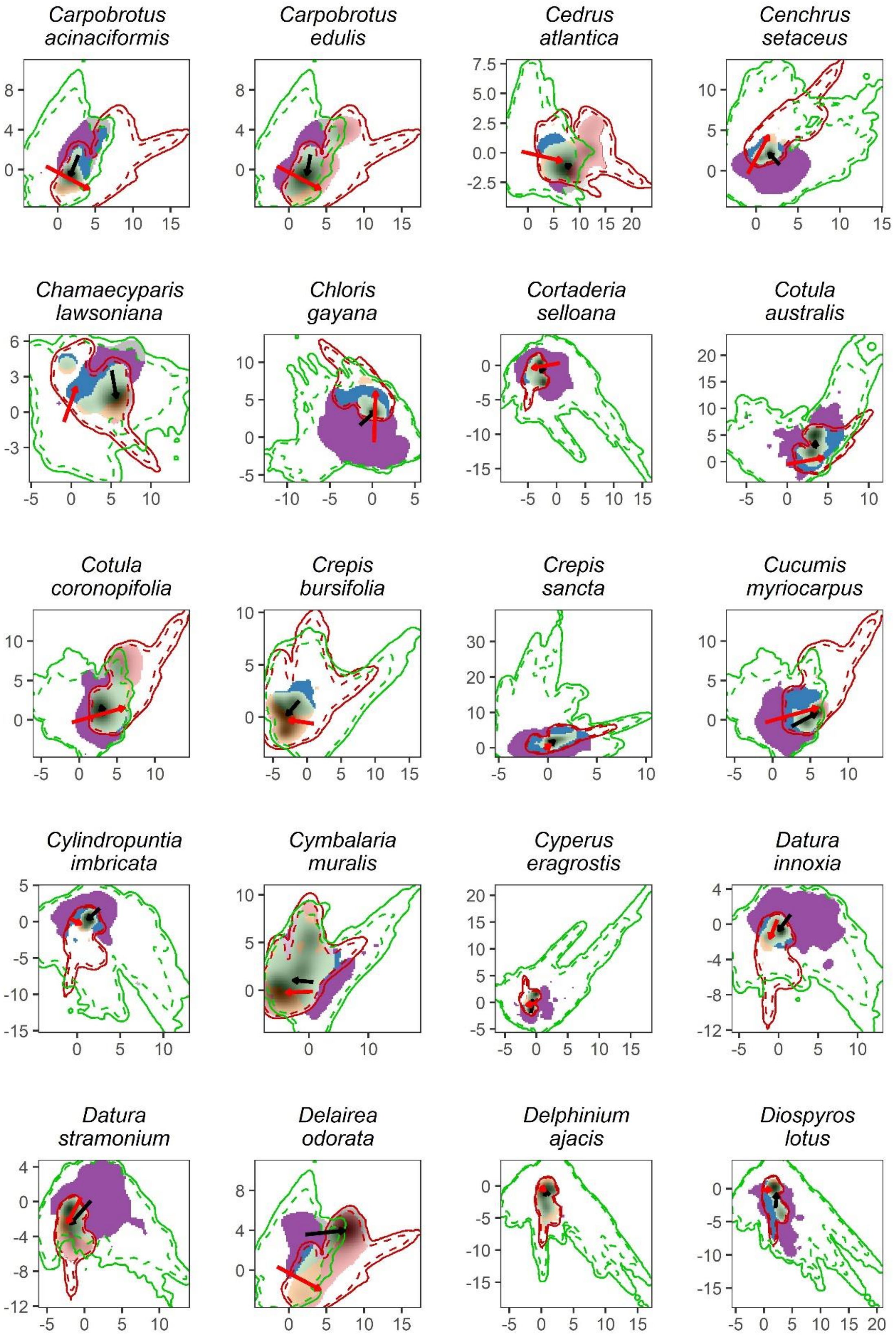
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Cortaderia selloana
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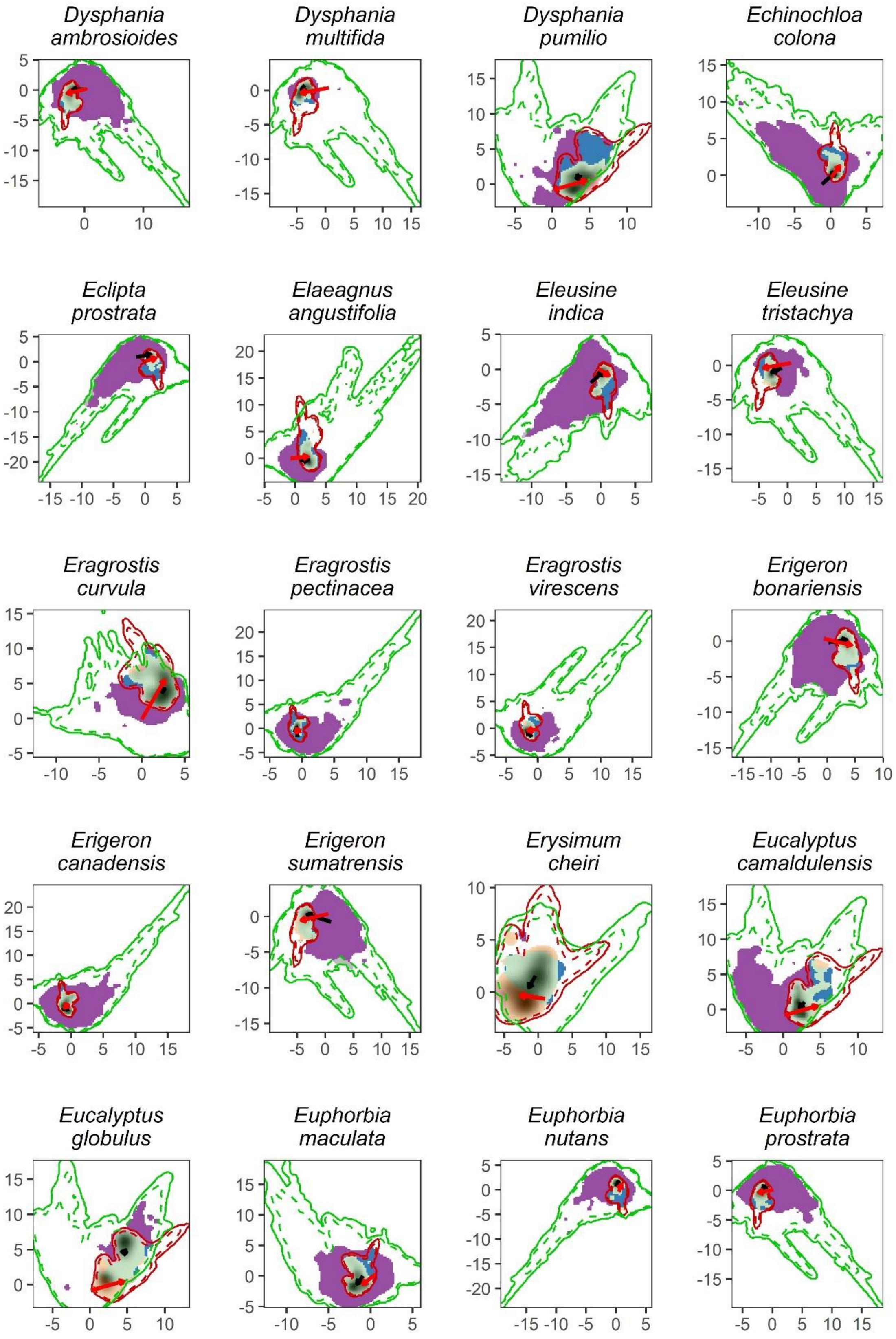
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Eleusine tristachya
Eragrostis curvula
Eragrostis pectinacea
Eragrostis virescens
Erigeron bonariensis
Erigeron canadensis
Erigeron sumatrensis
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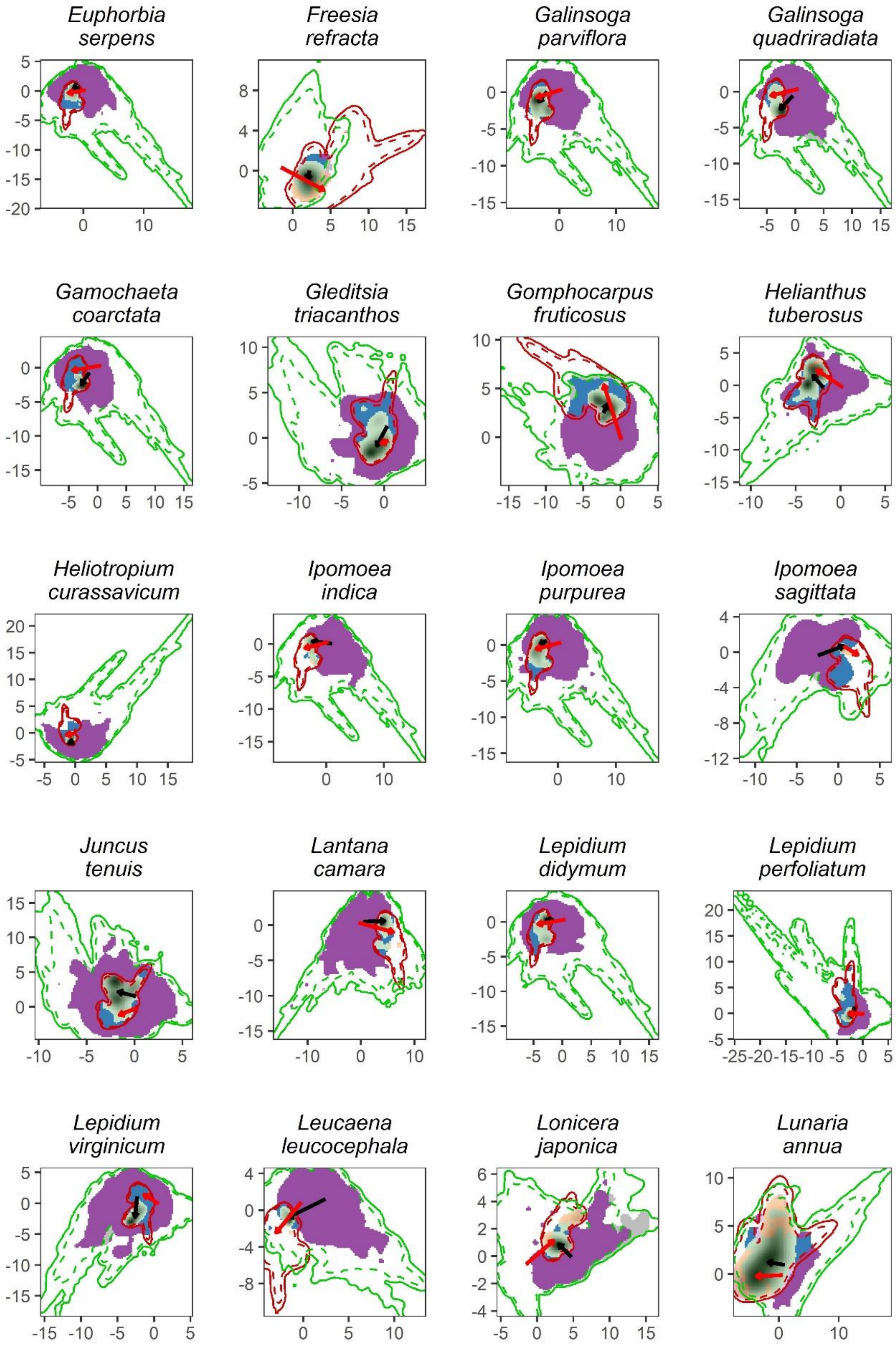
Eucalyptus globulus
Euphorbia maculata
Euphorbia nutans
Euphorbia prostrata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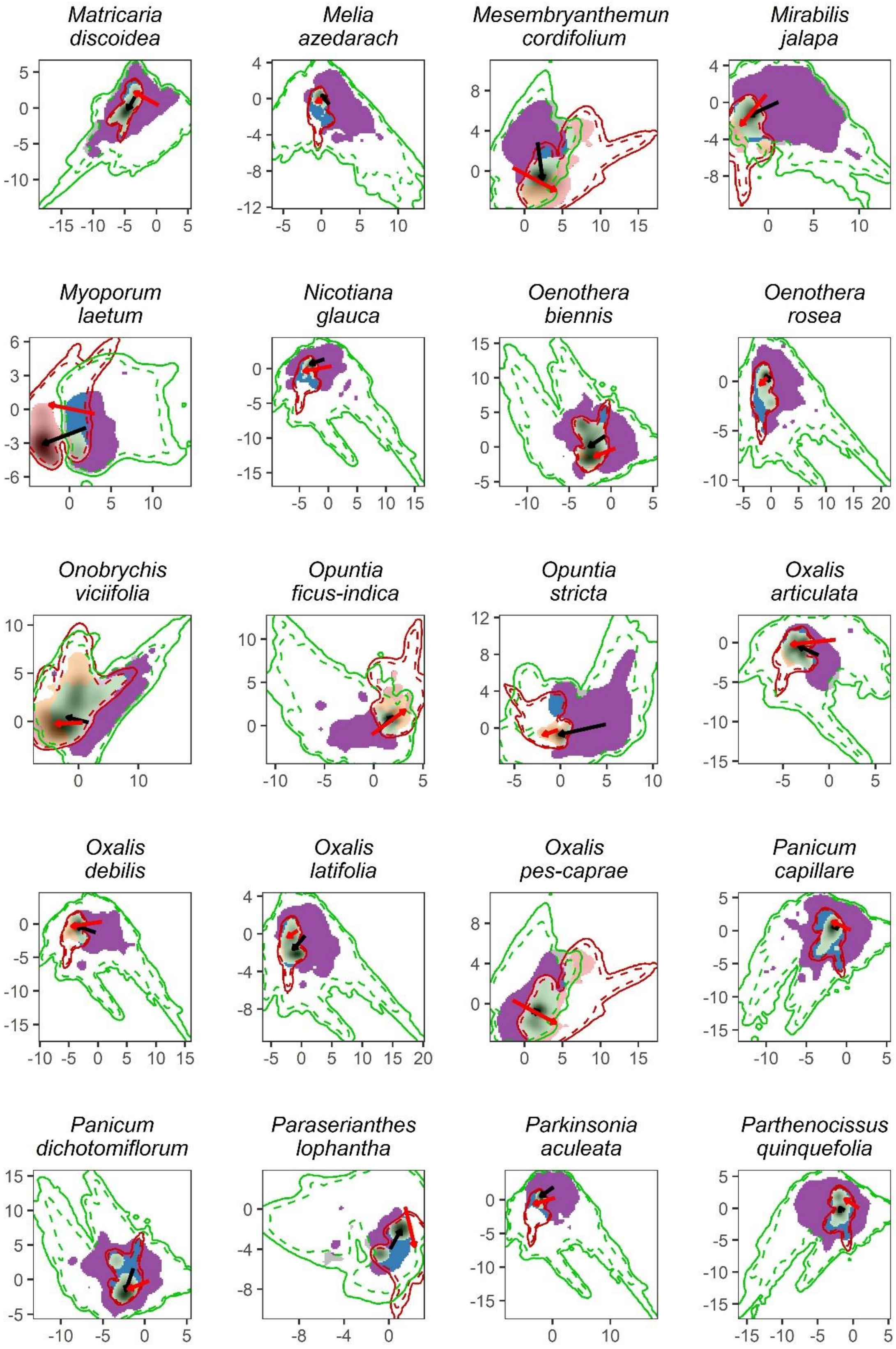
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Mesembryanthemun cordifolium
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0 5 10 15
Mirabilis jalapa
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0 5 10
Myoporum laetum
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0 5 10
Nicotiana glauca
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Oenothera biennis
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Oenothera rosea
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-5 0 5 10 15 20
Onobrychis viciifolia
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0 10
Opuntia ficus-indica
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Opuntia stricta
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Oxalis articulata
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Oxalis debilis
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Oxalis pes-caprae
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0 5 10 15
Panicum capillare
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Panicum dichotomiflorum
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Paraserianthes lophantha
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Parkinsonia aculeata
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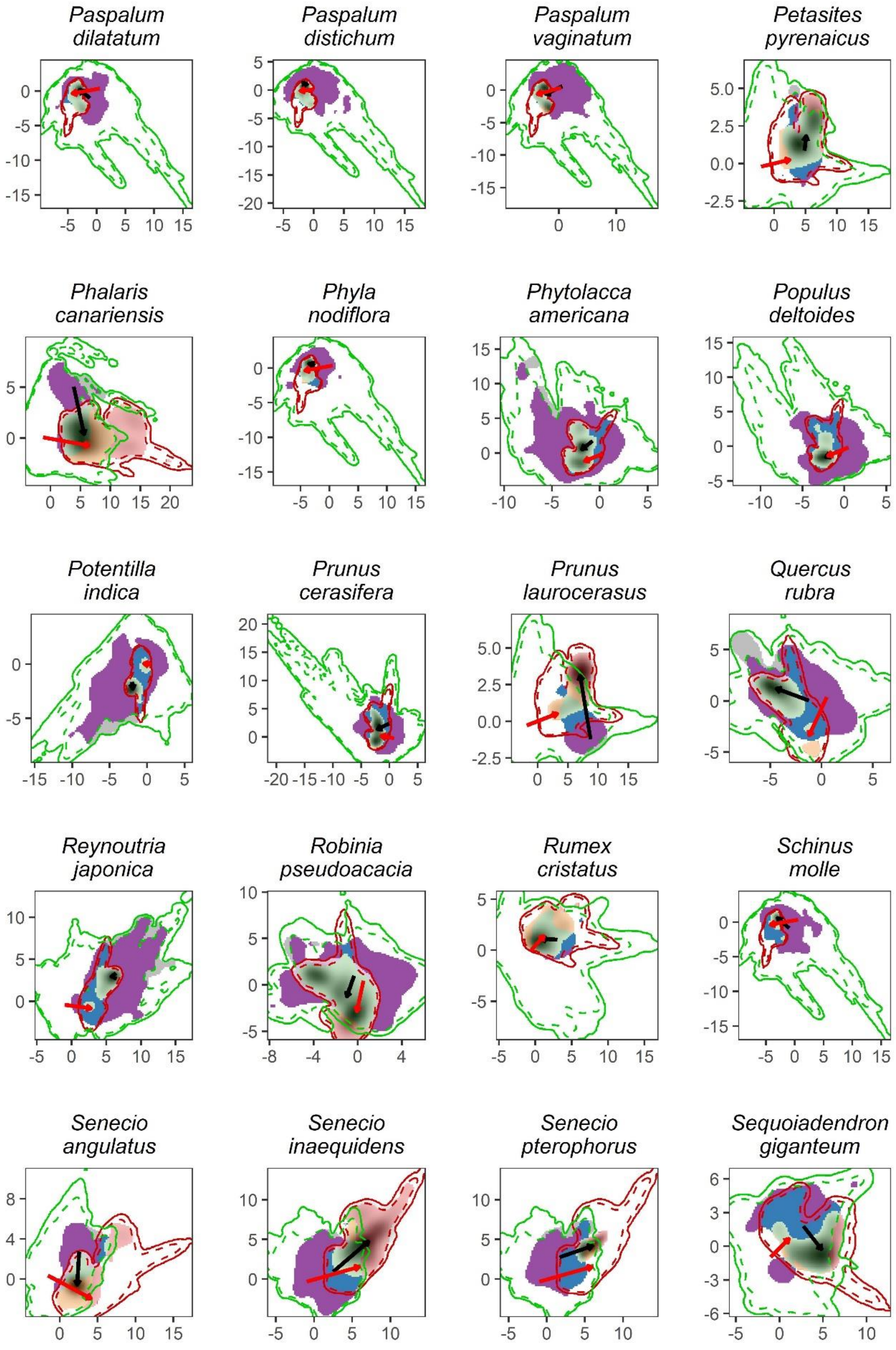
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Paspalum vaginatum
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0 10
Petasites pyrenaicus
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0 5 10 15
Phalaris canariensis
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Phyla nodiflora
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Potentilla indica
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Prunus laurocerasus
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0 5 10 15
Quercus rubra
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Reynoutria japonica
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Schinus molle
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Senecio angulatus
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0 5 10 15
Senecio inaequidens
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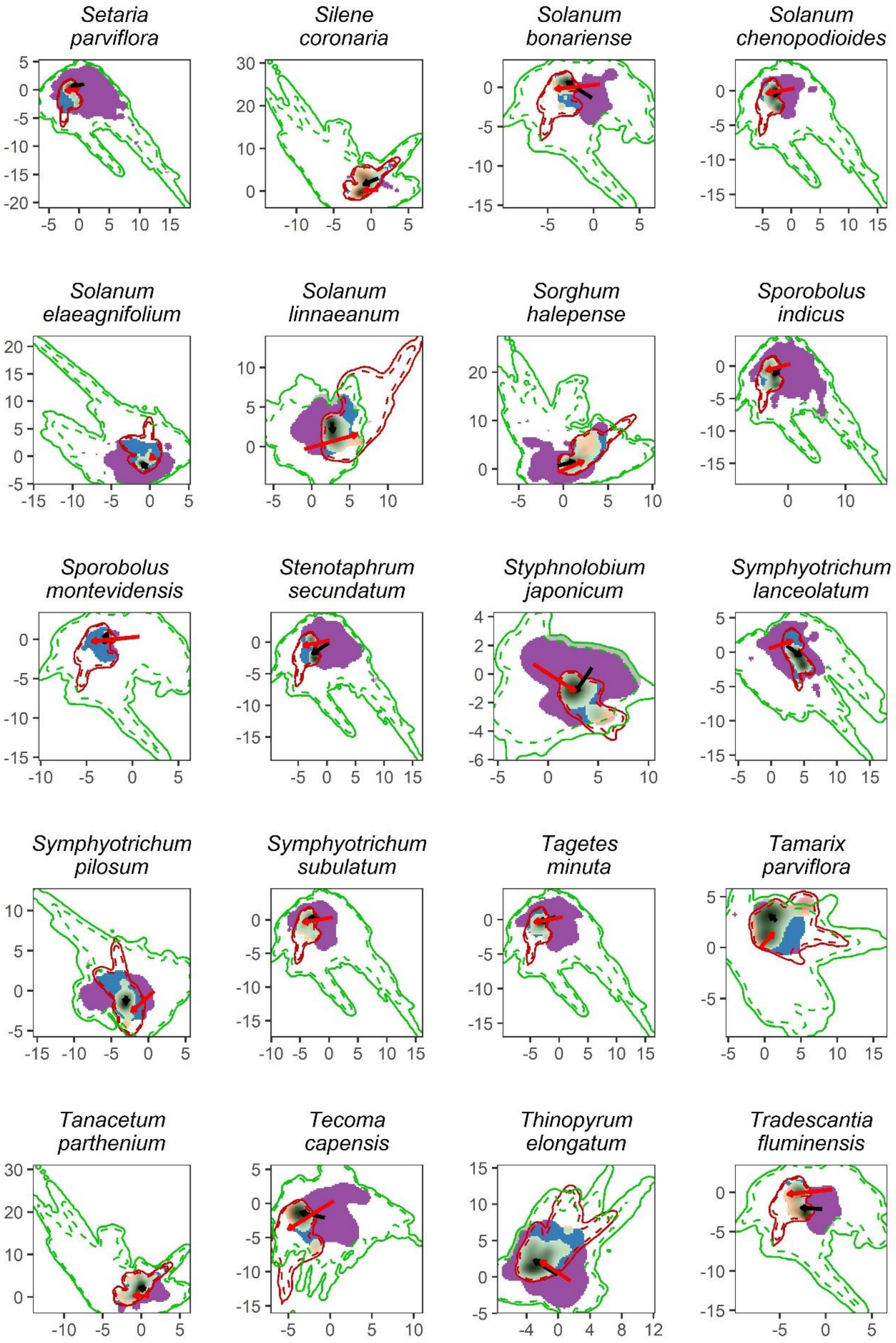
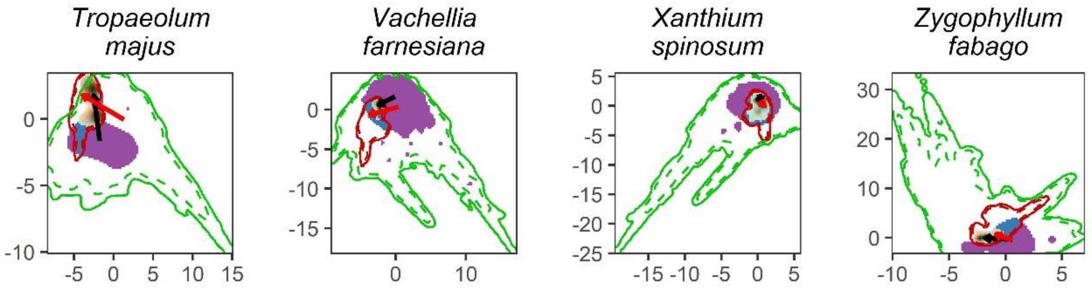

Setaria parviflora
Silene coronaria
Solanum bonariense
Solanum chenopodioides
Solanum elaeagnifolium
Solanum linnaeanum
Sorghum halepense
Sporobolus indicus
Sporobolus montevidensis
Stenotaphrum secundatum
Styphnolobium japonicum
Symphyotrichum lanceolatum
Symphyotrichum pilosum
Symphyotrichum subulatum
Tagetes minuta
Tamarix parviflora
Tanacetum parthenium
Tecoma capensis
Thinopyrum elongatum
Tradescantia fluminensis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5
0
-5
-10
-15
-20
-25
-15 -10 -5 0 5
Zygophyllum fabago
30
20
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