




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

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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 G_i^* 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.

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KEYWORDS

alien species, biological invasions, colonization pressure, hotspot, introduction pathways, large-scale dataset, minimum residence time, propagule pressure, spatial patterns

1 | 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 (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 (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 (e.g. 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 (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 | METHODS

2.1 | Study area

Catalonia (NE Spain) is a region of 32,000 km² located on the Mediterranean coast and bounded on the north by the Pyrenees (Figure 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 & Burriel, 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).

2.2 | 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 1,500, as there are many information gaps regarding those species introduced earlier (e.g. Chytrý et al., 2009; Giraldo-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

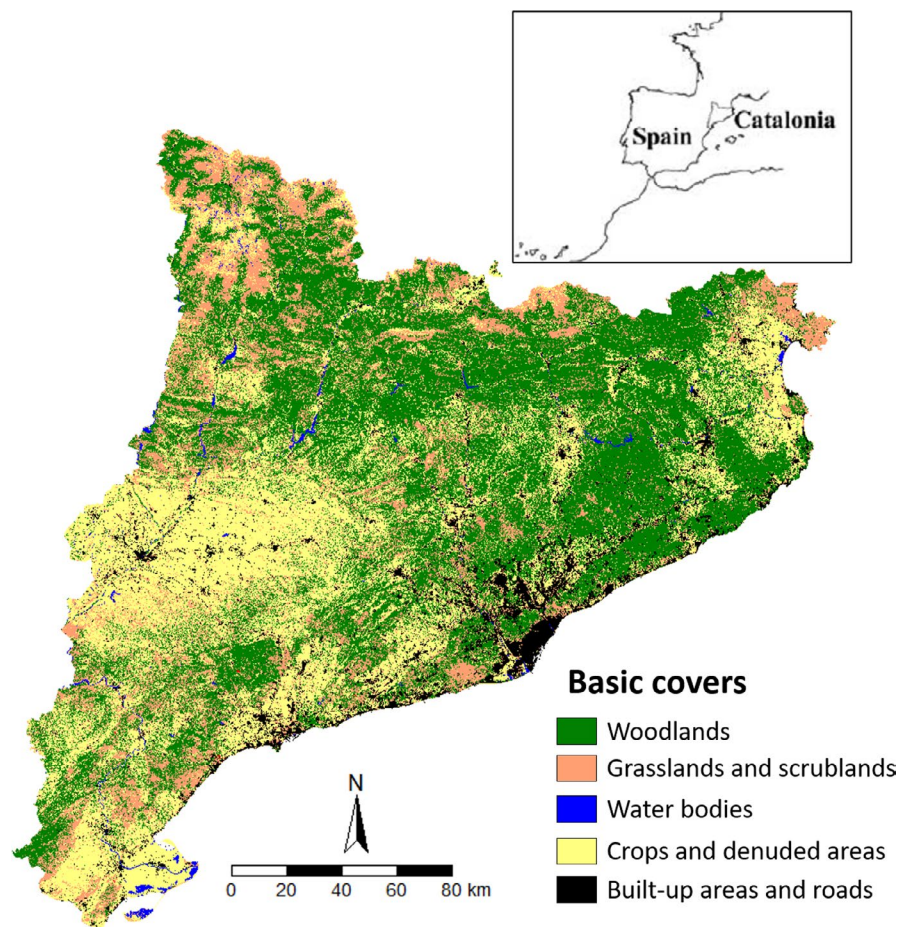


FIGURE 1 Basic land cover map of the study area, generalized from the land cover map of Catalonia (CREAF, 2009)

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., 2004). 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 Appendix S1). 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),

Variable (Abbreviation)	Units	Data source
Climatic		
		Digital Climatic Atlas of Catalonia, http://www.opengis.uab.cat/acdc/en_index.htm
Mean temperature (TEMP) ^a	°C	
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, CREAM, http://www.cream.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, CREAM, http://www.cream.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, CREAM, http://www.cream.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) ^a	m	

TABLE 1 Environmental variables related to pathway-specific species richness with their data sources

^aIndicates variables removed from the pool to control multicollinearity.

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 Gassó et al., 2009, 2010; Giraldo-Beltrán et al., 2015). We calculated MRT as the difference between 2019 and the year of first known record in our study area (see Appendix S1 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 (e.g. 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 1) based on previous studies, at 10-km UTM scale (Gassó et al., 2009; Giraldo-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., 2019; 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., 2019; 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).

2.3 | 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 \times group combinations (Table 2, Appendix S2). 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.

TABLE 2 Number of species introduced for each pathway across taxonomic groups (total number of species = 869)

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	

Note: Since some species ($n = 43$) have been introduced via two pathways, the sum of counts column-wise (43 species are counted twice) does not 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.

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 \times group combinations into a two-way contingency table (Table 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 ($0.3\text{--}0.7$) 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 (G_i^*) statistic. The G_i^* 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 G_i^* 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 ($p < .05/327 = p < .0001$).

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

TABLE 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)

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

Note: 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: $p > .05$).

Plants pool terrestrial ($n = 520$) and aquatic ($n = 27$) species.

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 (Appendix S3).

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 G_i^* 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).

3 | RESULTS

3.1 | 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). Most alien species had small range sizes (95% of them occupy less than half of our study area; Appendix S2).

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 3; Figure 2).

Among pathways (adjusted $R^2 = 0.351$), 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: $p > .05$; Table 3, Figure 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 (Figure 2).

Among taxonomic groups ($R^2 = 0.368$), the rate of spread was lowest for terrestrial invertebrates, with only plants spreading at a significantly faster rate (all other pairwise comparisons of slopes: $p > .05$; Table 3, Figure 2). Indeed, terrestrial invertebrates stood out as being the only taxonomic group with an almost flat slope (Figure 2). Results of additional groupings are presented in Appendix S4.

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%).

3.2 | 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 (Figure 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 (Figure 4). Congruence with hotspots of total alien species richness

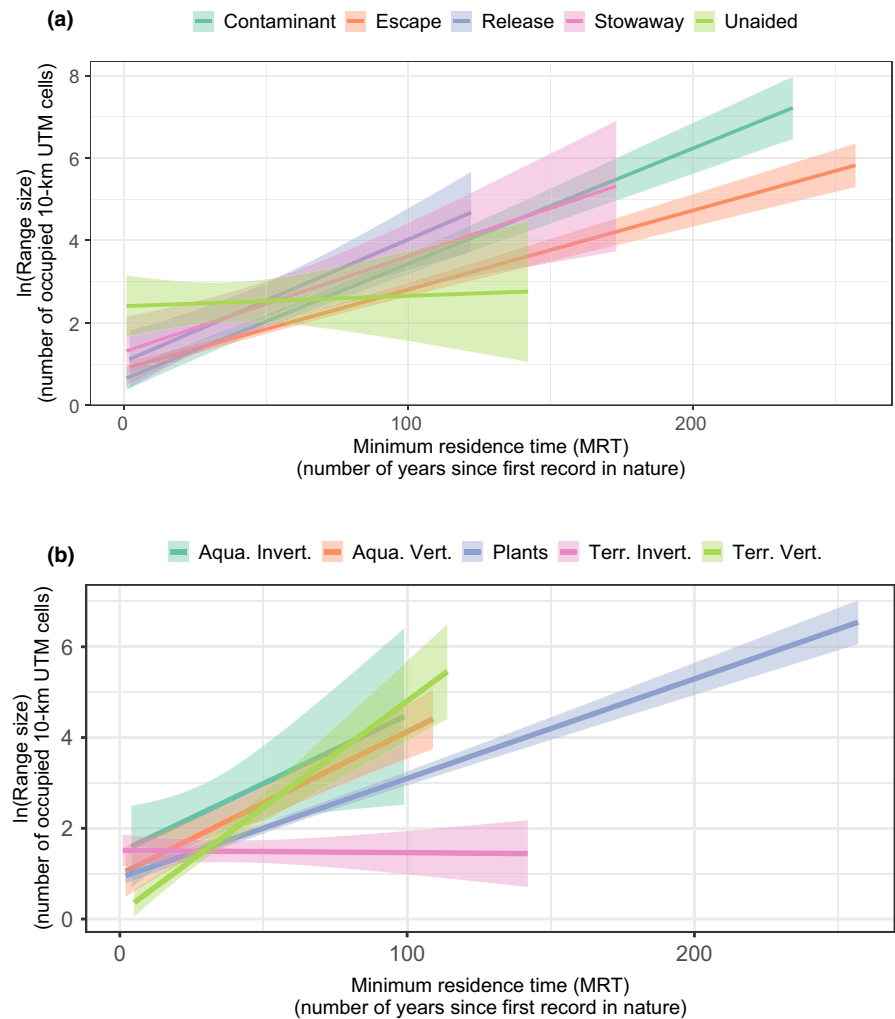


FIGURE 2 Range size of alien species in Catalonia ($n = 869$ species) in relation to the MRT for (a) each pathway, and (b) taxonomic group based on the ANCOVA models. Range size is ln-transformed. Shaded area indicates 95% confidence interval around linear regression slopes. Plants pool both terrestrial and aquatic plants. Abbreviations in panel (b): Aqua. = aquatic; Vert. = vertebrates; Invert. = invertebrates

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%).

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 (adjusted $R^2 = 0.60$, $p < .05$), 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 adjusted R^2 ; Borcard et al., 2011) in the RDA (Appendix S5). 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 (Figure 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.

4 | 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.

4.1 | Species range size across pathways and groups

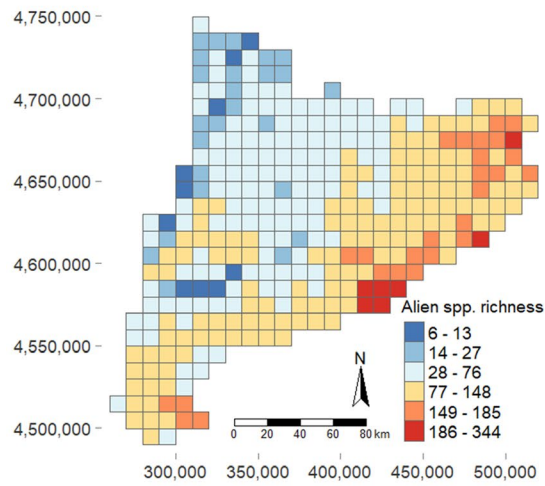
Unexpectedly, pathways were largely equivalent at determining range size (extensive overlap in range size over time, rejecting H1). Species introduced through the unaided pathway achieved the smallest ranges (almost no increase in range size over time), although their range sizes overlapped with those 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).

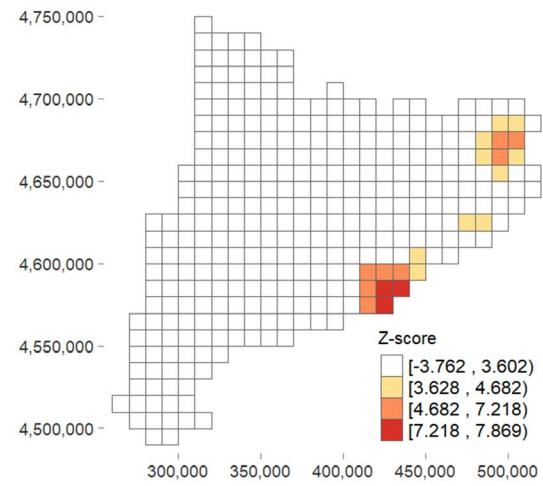
Nuances in the selection of species for transport could explain the lower range of the escape pathway compared to contaminant. Previous work with plants at large scales showed that cultivation led to a greater number of occupied regions (Guo et al., 2019; Pyšek et al. 2015). Nevertheless, a study in 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 et al., 2011; Pyšek, 1998), 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 (Giraldo-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; Table 2, Appendix S4). 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 (Figure 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

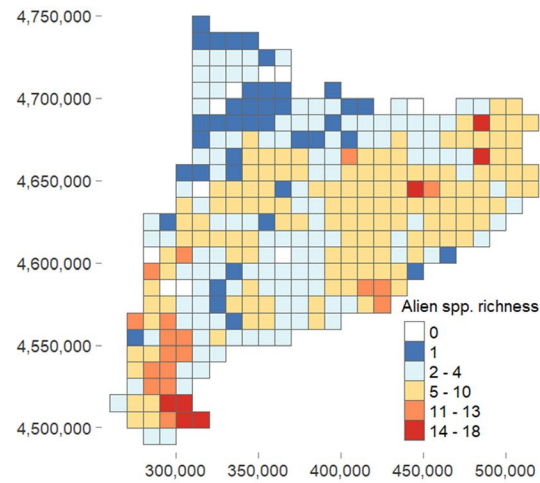
(a) Total (richness counts)



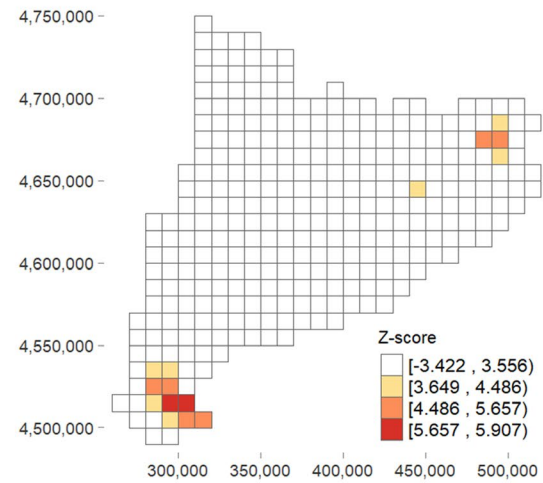
(b) Total (richness hotspots)



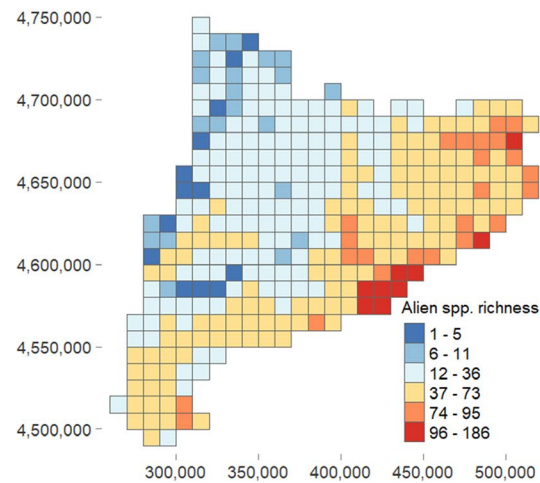
(c) Release (richness counts)



(d) Release (richness hotspots)



(e) Escape (richness counts)



(f) Escape (richness hotspots)

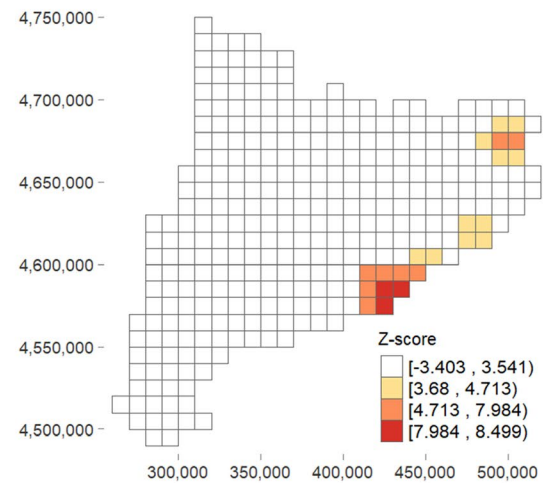
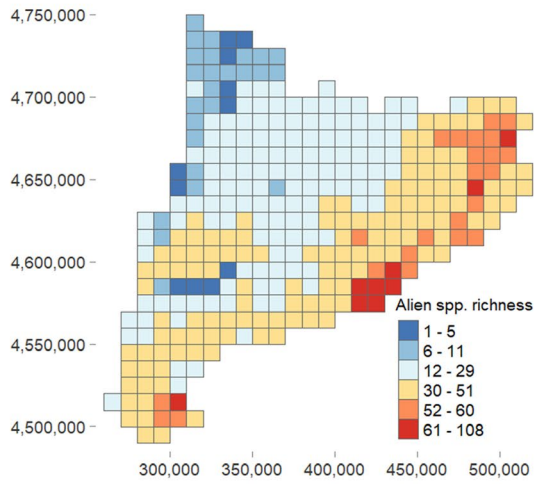
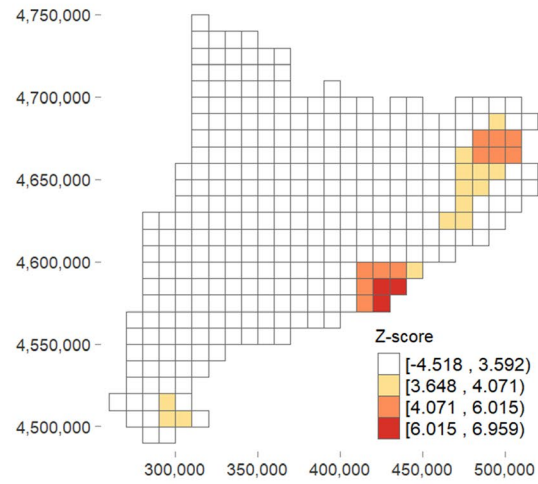


FIGURE 3 (Continued)

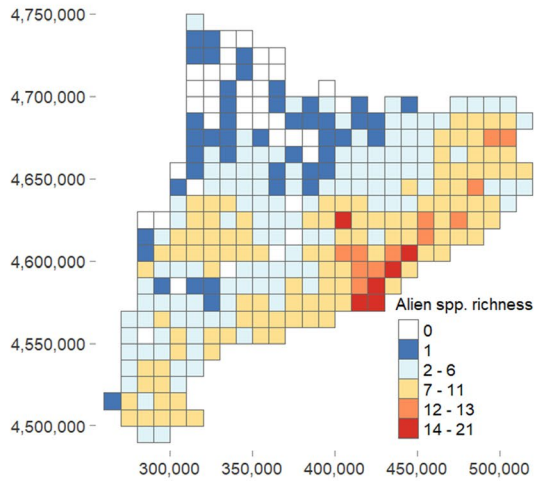
(g) Contaminant (richness counts)



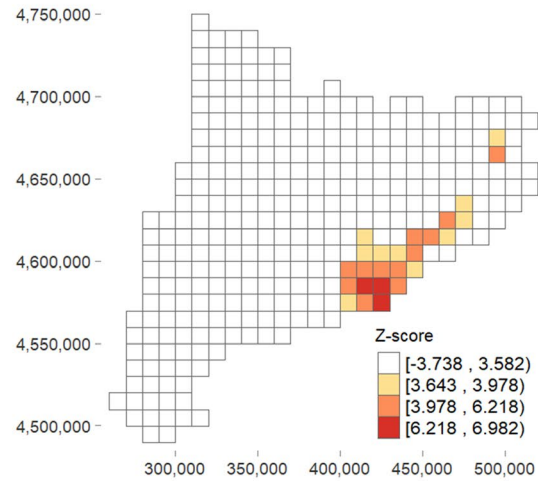
(h) Contaminant (richness hotspots)



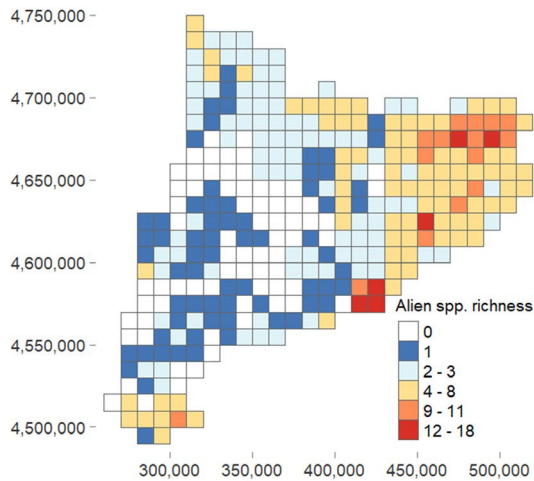
(i) Stowaway (richness counts)



(j) Stowaway (richness hotspots)



(k) Unaided (richness counts)



(l) Unaided (richness hotspots)

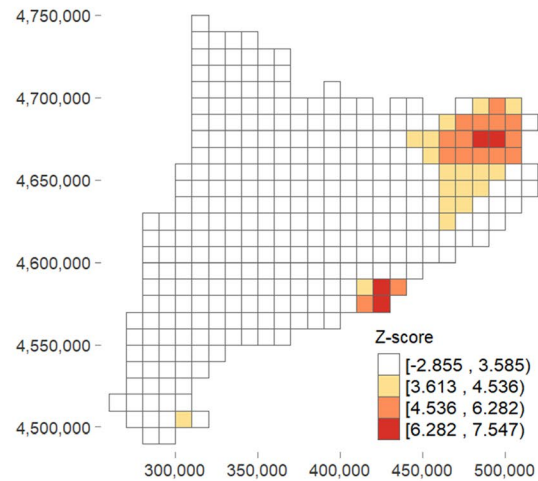


FIGURE 3 (Continued)

FIGURE 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

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, 2010; 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 et al., 2018). In comparison, human use of invertebrates is very limited, and thus, they are mostly introduced unintentionally (Rabitsch, 2010). 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).

4.2 | 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., 2019). 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, 2010). 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).

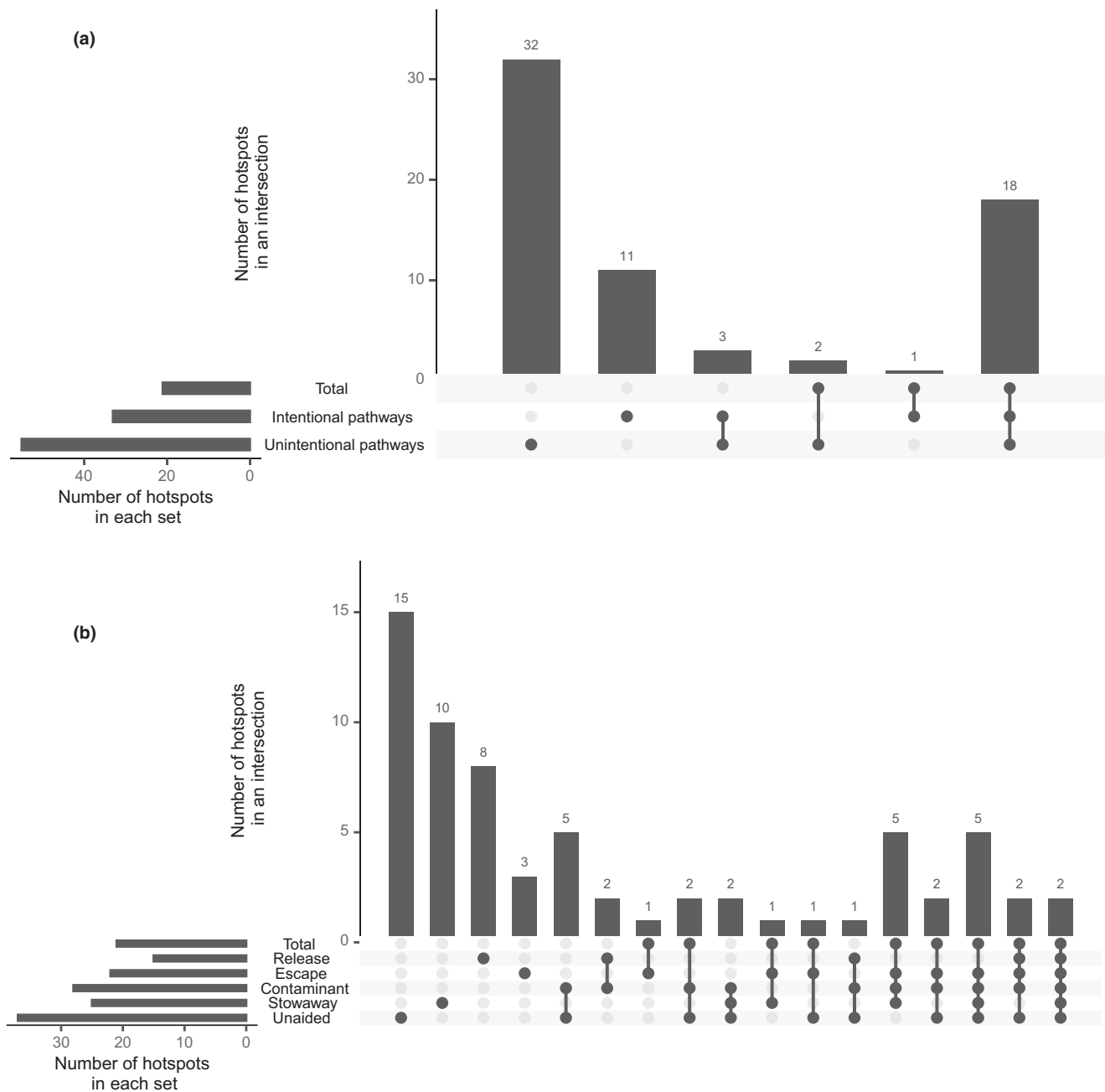


FIGURE 4 Assessment of spatial congruence through the intersection between sets of hotspots (number of different hotspots = 67), considering total species richness and pathway species richness, either: (a) grouping pathways by intentionality, or (b) considering each individual pathway. The number of 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)

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 (e.g. 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.

4.3 | Implications for management

Our work has explored how a standardized classification of pathways can be used in conjunction with spatially and temporally

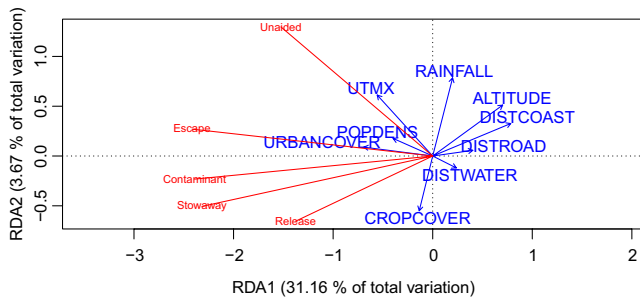


FIGURE 5 RDA correlation biplot, featuring the first two canonical axes (35% of total variation). Explanatory variables follow the abbreviations in Table 1. This analysis is restricted to 10-km UTM cells with more than 40% of their surface on Catalan land ($n = 327$ cells)

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 \times 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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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13251>.

DATA AVAILABILITY STATEMENT

Data available from the Supporting Information of this paper and the public database EXOCAT (http://exocatdb.creaf.cat/base_dades/).

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REFERENCES

- Bielsa, I., Pons, X., & Bunce, B. (2005). Agricultural abandonment in the North Eastern Iberian Peninsula: The use of basic landscape metrics to support planning. *Journal of Environmental Planning and Management*, 48, 85–102. <https://doi.org/10.1080/0964056042000308166>
- Bivand, R. S., & Wong, D. W. S. (2018). Comparing implementations of global and local indicators of spatial association. *TEST*, 27, 716–748. <https://doi.org/10.1007/s11749-018-0599-x>
- Blackburn, T. M., Cassey, P., & Duncan, R. P. (2019). Colonization pressure: A second null model for invasion biology. *Biological Invasions*, 22, 1221–1233. <https://doi.org/10.1007/s10530-019-02183-7>
- Blackburn, T. M., Lockwood, J. L., & Cassey, P. (2015). The influence of numbers in invasion success. *Molecular Ecology*, 24, 1942–1953. <https://doi.org/10.1111/mec.13075>
- Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R. Use R! series*. Springer Science.
- Catalan Water Agency. (2005). *Caracterització de masses d'aigua i anàlisi del risc d'incompliment dels objectius de la directiva marc de l'aigua (2000/60/ce) a Catalunya (conques intra i intercomunitàries)*. En compliment als articles 5, 6 i 7 de la Directiva. Generalitat de Catalunya, Departament de Territori i Medi Ambient.
- Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L. C., & Vilà, M. (2009). European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, 15, 98–107. <https://doi.org/10.1111/j.1472-4642.2008.00515.x>
- Clavero, M., & García-Berthou, E. (2006). Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. *Ecological Applications*, 16, 2313–2324. [https://doi.org/10.1890/1051-0761\(2006\)016\[2313:HDAIRO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[2313:HDAIRO]2.0.CO;2)
- Convention on Biological Diversity (2011). *The strategic plan for biodiversity 2011–2020 and the Aichi biodiversity targets*. UNEP/CBD/COP/DEC/X/2, 29 October 2010, Nagoya, Japan. COP CBD Tenth Meeting. Retrieved from www.cbd.int/decisions/cop/?m=cop-10
- Convention on Biological Diversity. (2014). *Pathways of introduction of invasive species, their prioritization and management*. Note by the Executive Secretary. Eighteenth Meeting of the Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA). – Montreal, 23–28 June 2014. Retrieved from www.cbd.int/doc/meetings/sbstta/sbstta-18/official/sbstta-18-09-add1-en.pdf
- Crosby, A. W. (2004). *Ecological imperialism. The biological expansion of Europe, 900–1900* (2nd ed.). Cambridge University Press.

- Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T. M., Dyer, E. E., Cassey, P., Scrivens, S. L., Economo, E. P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., ... Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, 1, 186. <https://doi.org/10.1038/s41559-017-0186>
- Dyer, E. E., Franks, V., Cassey, P., Collen, B., Cope, R. C., Jones, K. E., Şekercioğlu, Ç. H., & Blackburn, T. M. (2016). A global analysis of the determinants of alien geographical range size in birds. *Global Ecology and Biogeography*, 25, 1346–1355. <https://doi.org/10.1111/geb.12496>
- Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., Gonzalez, P., Grosholz, E. D., Ibañez, I., Miller, L. P., Sorte, C. J. B., & Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, 7, 12485. <https://doi.org/10.1038/ncomms12485>
- Essl, F., Bacher, S., Blackburn, T. M., Booy, O., Brundu, G., Brunel, S., Cardoso, A.-C., Eschen, R., Gallardo, B., Galil, B., García-Berthou, E., Genovesi, P., Groom, Q., Harrower, C., Hulme, P. E., Katsanevakis, S., Kenis, M., Kühn, I., Kumschick, S., ... Jeschke, J. M. (2015). Crossing frontiers in tackling pathways of biological invasions. *BioScience*, 65, 769–782. <https://doi.org/10.1093/biosci/biv082>
- Faulkner, K. T., Robertson, M. P., Rouget, M., & Wilson, J. R. U. (2016). Understanding and managing the introduction pathways of alien taxa: South Africa as a case study. *Biological Invasions*, 18, 73–87. <https://doi.org/10.1007/s10530-015-0990-4>
- García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G., & Feo, C. (2005). Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 453–463. <https://doi.org/10.1139/f05-017>
- Gassó, N., Pyšek, P., Vilà, M., & Williamson, M. (2010). Spreading to a limit: The time required for a neophyte to reach its maximum range. *Diversity and Distributions*, 16, 310–311. <https://doi.org/10.1111/j.1472-4642.2010.00647.x>
- Gassó, N., Sol, D., Pino, J., Dana, E. D., Lloret, F., Sanz-Elorza, M., Sobrino, E., & Vilà, M. (2009). Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distributions*, 15, 50–58. <https://doi.org/10.1111/j.1472-4642.2008.00501.x>
- Gehlenborg, N. (2019). *UpSetR: A More Scalable Alternative to Venn and Euler Diagrams for Visualizing Intersecting Sets*. R package version 1.4.0. Retrieved from <https://CRAN.R-project.org/package=UpSetR>
- Getis, A., & Ord, J. K. (1992). The analysis of spatial association by use of distance statistics. *Geographical Analysis*, 24, 189–206. <https://doi.org/10.1111/j.1538-4632.1992.tb00261.x>
- Gippet, J. M. W., Liebhold, A. M., Fenn-Moltu, G., & Bertelsmeier, C. (2019). Human-mediated dispersal in insects. *Current Opinion in Insect Science*, 35, 96–102. <https://doi.org/10.1016/j.cois.2019.07.005>
- Giraldo-Beltrán, P., Andreu, J., & Pino, J. (2015). Exploring changes in the invasion pattern of alien flora in Catalonia (NE of Spain) from large datasets. *Biological Invasions*, 17, 3015–3028. <https://doi.org/10.1007/s10530-015-0930-3>
- Guo, W.-Y., van Kleunen, M., Pierce, S., Dawson, W., Essl, F., Kreft, H., Maurel, N., Pergl, J., Seebens, H., Weigelt, P., & Pyšek, P. (2019). Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization. *Global Ecology and Biogeography*, 28, 628–639. <https://doi.org/10.1111/geb.12882>
- Haran, J., Roques, A., Bernard, A., Robinet, C., & Roux, G. (2015). Altitudinal barrier to the spread of an invasive species: Could the Pyrenean chain slow the natural spread of the Pinewood Nematode? *PLoS One*, 10, e0134126. <https://doi.org/10.1371/journal.pone.0134126>
- Harrower, C. A., Scalerà, R., Pagad, S., Schonrogge, K., & Roy, H. E. (2018). *Guidance for interpretation of CBD categories on introduction pathways*. Report to the European Commission: Retrieved from <https://circa.bc.europa.eu/w/browse/O606f9b8-b567-4f53-9bc8-76e7800f0971>
- Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W., & Vilà, M. (2008). Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology*, 45, 403–414. <https://doi.org/10.1111/j.1365-2664.2007.01442.x>
- Iannone, B. V., Potter, K. M., Guo, Q., Liebhold, A. M., Pijanowski, B. C., Oswalt, C. M., & Fei, S. (2016). Biological invasion hotspots: A trait-based perspective reveals new sub-continental pattern. *Ecography*, 39, 961–969. <https://doi.org/10.1111/ecog.01973>
- Ibañez, J. J., & Burriel, J. A. (2010). Mapa de cubiertas del suelo de Cataluña: características de la tercera edición y relación con SIOSE. In J. Ojeda, M. F. Pita, & I. Vallejo (Eds.), *Tecnologías de la información geográfica: La información geográfica al servicio de los ciudadanos* (pp. 179–198). Secretariado de Publicaciones de la Universidad de Sevilla.
- Ibañez, J. J., Burriel, J. A., & Pons, X. (2002). El mapa de cobertes del sòl de Catalunya: Una eina per al coneixement, la planificació i la gestió del territori. *Perspectives Territorials*, 3, 10–25.
- Lenth, R. (2020). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.5.2-1. Retrieved from <https://CRAN.R-project.org/package=emmeans>
- Llurdés, J. C., Priestley, G. K., & Romagosa, F. (2009). *Informe del sector del turisme (document de treball)*. Document elaborat per l'Escola Universitària de Turisme i Direcció d'Hosteleria (centre adscrit a l'UAB). Retrieved from http://www.gencat.cat/mediamb/publicacions/Estudis/EDIS_sector_turisme.pdf
- Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, 20, 223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2009). The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, 15, 904–910. <https://doi.org/10.1111/j.1472-4642.2009.00594.x>
- Martínez, J. P., & Montserrat, P. (1990). Biogeographic features of the Pyrenean range. *Mountain Research and Development*, 10, 235–240. <https://doi.org/10.2307/3673603>
- McGeoch, M. A., Genovesi, P., Bellingham, P. J., Costello, M. J., McGrannachan, C., & Sheppard, A. (2016). Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. *Biological Invasions*, 18, 299–314. <https://doi.org/10.1007/s10530-015-1013-1>
- Ninyerola, M., Pons, X., & Roure, J. M. (2000). A methodological approach of climatological modelling of air temperature and precipitation. *International Journal of Climatology*, 20, 1823–1841. [https://doi.org/10.1002/1097-0088\(20001130\)20:14<1823::AID-JOC566>3.0.CO;2-B](https://doi.org/10.1002/1097-0088(20001130)20:14<1823::AID-JOC566>3.0.CO;2-B)
- Nunes, A. L., Tricarico, E., Panov, V. E., Cardoso, A. C., & Katsanevakis, S. (2015). Pathways and gateways of freshwater invasions in Europe. *Aquatic Invasions*, 10, 359–370. <https://doi.org/10.3391/ai.2015.10.4.01>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2019). *vegan: community ecology package*. R package version 2.5-6. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Ord, J. K., & Getis, A. (1995). Local spatial autocorrelation statistics: Distributional issues and an application. *Geographical Analysis*, 27, 286–306. <https://doi.org/10.1111/j.1538-4632.1995.tb00912.x>
- Padayachee, A. L., Irllich, U. M., Faulkner, K. T., Gaertner, M., Procheş, Ş., Wilson, J. R. U., & Rouget, M. (2017). How do invasive species travel to and through urban environments? *Biological Invasions*, 19, 3557–3570. <https://doi.org/10.1007/s10530-017-1596-9>
- Palazón, S., Durà, C., & Ventura, J. (2015). Situación actual del coipú, un mamífero exótico semiacuático, en Catalunya. *Galemys*, 27, 63–66. <https://doi.org/10.7325/Galemys.2015.N2>

- Pergl, J., Pyšek, P., Bacher, S., Essl, F., Genovesi, P., Harrower, C. A., Hulme, P. E., Jeschke, J. E., Kenis, M., Kühn, I., Perglová, I., Rabitsch, W., Roques, A., Roy, D. B., Roy, H. E., Vilà, M., Winter, M., & Nentwig, W. (2017). Troubling travellers: Are ecologically harmful alien species associated with particular introduction pathways? *Neobiota*, 32, 1–20. <https://doi.org/10.3897/neobiota.32.10199>
- Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, 52, 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- Pino, J., Font, X., Carbó, J., Jové, M., & Pallerès, L. (2005). Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological Conservation*, 122, 339–350. <https://doi.org/10.1016/j.biocon.2004.08.006>
- Pons, X. (2002). *MiraMon. Sistema d'Informació Geogràfica i software de Teledetecció*. Centre de Recerca Ecològica i Aplicacions Forestals, CREAF, Bellaterra. Retrieved from <https://www.creaf.uab.es/mirammon/>
- Procheş, Ş., Wilson, J. R. U., Richardson, D. M., & Rejmánek, M. (2012). Native and naturalized range size in Pinus: Relative importance of biogeography, introduction effort and species traits. *Global Ecology and Biogeography*, 21, 513–523. <https://doi.org/10.1111/j.1466-8238.2011.00703.x>
- Pyšek, P., Jarosik, V., Hulme, P. E., Kuhn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didziulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P. W., Desprez-Loustau, M.-L., Nentwig, W., Pergl, J., Paboljsaj, K., ... Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 12157–12162. <https://doi.org/10.1073/pnas.1002314107>
- Pyšek, P., Jarošík, V., & Pergl, J. (2011). Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as a threat to natural areas. *PLoS One*, 6(9), e24890. <https://doi.org/10.1371/journal.pone.0024890>
- Pyšek, P., Lambdon, P. W., Arianoutsou, M., Kühn, I., Pino, J., & Winter, M. (2009). Alien vascular plants of Europe. In DAISIE (Ed.), *Handbook of Alien Species in Europe. Invading nature: Springer series in invasion ecology* (Vol. 3, pp. 43–61). Springer.
- Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M., Sádlo, J., Suda, J., Tichý, L., & Kühn, I. (2015). Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology*, 96, 762–774. <https://doi.org/10.1890/14-1005.1>
- Pyšek, P., & Pyšek, P. (1998). Is there a taxonomic pattern to plant invasions? *Oikos*, 82, 282–294. <https://doi.org/10.2307/3546968>
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Rabitsch, W. (2010). Pathways and vectors of alien arthropods in Europe. Chapter 3. In A. Roques, M. Kenis, D. Lees, C. Lopez-Vaamonde, W. Rabitsch, J.-Y. Rasplus, & D. Roy (Eds.), *Alien terrestrial arthropods of Europe. Biodiversity and Ecosystem Risk Assessment*, 4, 27–43. <https://doi.org/10.3897/biorisk.4.60>
- Rejmánek, M. (2000). Invasive plants: Approaches and predictions. *Austral Ecology*, 25, 497–506. <https://doi.org/10.1046/j.1442-9993.2000.01080.x>
- Roques, A. (2010). Taxonomy, time and geographic patterns. Chapter 2. In A. Roques, M. Kenis, D. Lees, C. Lopez-Vaamonde, W. Rabitsch, J.-Y. Rasplus, & D. Roy (Eds.), *Alien terrestrial arthropods of Europe. Biodiversity and Ecosystem Risk Assessment*, 4, 11–26. <https://doi.org/10.3897/biorisk.4.70>
- Roura-Pascual, N., Bas, J. M., Thuiller, W., Hui, C., Krug, R. M., & Brotons, L. (2009). From introduction to equilibrium: Reconstructing the invasive pathways of the Argentine ant in a Mediterranean region. *Global Change Biology*, 15, 2101–2115. <https://doi.org/10.1111/j.1365-2486.2009.01907.x>
- Sanz-Elorza, M., Dana, E. D., & Sobrino, E. (Eds.). (2004). *Atlas de las plantas alóctonas invasoras en España*. Madrid: Dirección General para la Biodiversidad. Retrieved from https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/inventario-nacional-de-biodiversidad/ieet_flora_vasc_aloctx_invas.aspx
- Saul, W.-C., Roy, H. E., Booy, O., Carnevali, L., Chen, H.-J., Genovesi, P., Harrower, C. A., Hulme, P. E., Pagad, S., Pergl, J., & Jeschke, J. M. (2017). Assessing patterns in introduction pathways of alien species by linking major invasion data bases. *Journal of Applied Ecology*, 54, 657–669. <https://doi.org/10.1111/1365-2664.12819>
- Signorell, A., Aho, K., Alfons, A., Anderegg, N., Aragon, T., Arachchige, C., Arppe, A., Baddeley, A., Barton, K., Bolker, B., Borchers, H. W., Caeiro, F., Champely, S., Chessel, D., Chhay, L., Cooper, N., Cummins, C., Dewey, M., Doran, H. C., & Zeileis, A. (2020). *DescTools: Tools for descriptive statistics*. R package version 0.99.38. Retrieved from <https://cran.r-project.org/web/packages/DescTools/>
- Turbelin, A. J., Malamud, B. D., & Francis, R. A. (2017). Mapping the global state of invasive alien species: Patterns of invasion and policy responses. *Global Ecology and Biogeography*, 26, 78–92. <https://doi.org/10.1111/geb.12517>
- Uller, T., & Leimu, R. (2011). Founder events predict changes in genetic diversity during human-mediated range expansions. *Global Change Biology*, 17, 3478–3485. <https://doi.org/10.1111/j.1365-2486.2011.02509.x>
- van Kleunen, M., Essl, F., Pergl, J., Brundu, G., Carboni, M., Dullinger, S., Early, R., González-Moreno, P., Groom, Q. J., Hulme, P. E., Kueffer, C., Kühn, I., Mágua, C., Maurel, N., Novoa, A., Parepa, M., Pyšek, P., Seebens, H., Tanner, R., ... Dehnen-Schmutz, K. (2018). The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews*, 93, 1421–1437. <https://doi.org/10.1111/brv.12402>
- Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., & Hulme, P. E. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8, 135–144. <https://doi.org/10.1890/080083>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Von der Lippe, M., & Kowarik, I. (2012). Interactions between propagule pressure and seed traits shape human-mediated seed dispersal along roads. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 123–130. <https://doi.org/10.1016/j.ppees.2011.09.006>
- Ward, S. F., Fei, S., & Liebhold, A. M. (2019). Spatial patterns of discovery points and invasion hotspots of non-native forest pests. *Global Ecology and Biogeography*, 28, 1749–1762. <https://doi.org/10.1111/geb.12988>
- Williamson, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., Stout, J., & Pyšek, P. (2009). The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions*, 15, 158–166. <https://doi.org/10.1111/j.1472-4642.2008.00528.x>
- Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: Dispersal pathways affect invasion success. *Trends in Ecology and Evolution*, 24, 136–144. <https://doi.org/10.1016/j.tree.2008.10.007>
- Wilson, J. R. U., Richardson, D. M., Rouget, M., Procheş, Ş., Amis, M. A., Henderson, L., & Thuiller, W. (2007). Residence time and potential range: Crucial considerations in modelling plant invasions. *Diversity and Distributions*, 13, 11–22. <https://doi.org/10.1111/j.1366-9516.2006.00302.x>

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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