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Evaluating the role of trophic interactions on forest restoration and resilience under global change

Miriam Selwyn Álvarez

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Evaluating the role of trophic interactions on forest restoration and resilience under global change

Doctoral Thesis

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To apply for the degree of Doctor

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“Many different checks come into play,
all concurring in determining the average number
or even the existence of the species.
I believe climate is to be the most effective of all checks.
But… What a struggle between the several kinds of trees
must here have gone on during long centuries,
each annually scattering its seeds by the thousand;
what war between insect and insect –
between insects, snails,
and other animals with birds and beasts of prey –
all striving to increase,
and all feeding on each other or
on the trees or their seeds and seedlings.
Throw up a handful of feathers,
and all must fall to the ground according to definite laws;
but how simple is this problem
compared to the action and reaction of the innumerable plants and animals
which have determined, in the course of centuries,
the proportional numbers and kinds of trees now growing.
The structure of every organic being is related,
in the most essential yet often hidden manner,
to that of all other organic beings,
with which it comes into competition for food or residence,
or from which it has to escape,
or on which it preys”.

Charles Darwin

The Origin of Species

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Abstract

The conversion and destruction of natural areas for agricultural use is a common form of land use change that leads to significant ecosystem degradation worldwide. This issue is exacerbated by the dual crisis of climate change and biodiversity loss, marked by rising temperatures and increased disturbance events such as flooding and extreme droughts. These factors, along with habitat destruction and species extinction, highlight the urgent need for initiatives to restore ecosystems and enhance their resilience. Efforts in this field have grown over the past decades, driven by the pressing need to combat land degradation. However, during the development of restoration initiatives, various obstacles are often encountered, leading to instances where restoration efforts fail to sustain their benefits over time highlighting the need to assess the outcomes of restoration actions and their underpinning mechanisms to ensure ecosystem resilience to environmental change.

In this thesis, we aimed at exploring these issues for the case of forest ecosystems, by investigating the role of seed dispersal in forest restoration success, the factors that influence the recovery of tree species diversity and whether resilience to disturbances is enhanced in novel restoration approaches such as rewilding efforts. To achieve this goal, we conducted three different analytical approaches: a systematic review (Chapter 2), a modelling approach based on a long-term monitoring scheme (Chapter 3), and a meta-analysis (Chapter 4).

In Chapter 2 we reviewed 157 articles to identify the most relevant intrinsic and extrinsic factors which influence the animal-mediated seed dispersal process and their contribution for forest restoration success globally and for different biomes. Intrinsic factors for successful restoration included seed traits (e.g., seed size) and dispersal distance ability, but also extrinsic factors such as the environmental characteristics (e.g., connectivity) and types of restoration conducted (e.g., active *vs.* passive restoration) influenced restoration success. Our results also highlighted the importance of distinguishing among biome types as differences arose regarding the main intrinsic and extrinsic factors determining successful restoration.

Given the importance of animal seed dispersal in restoration processes, as discussed in Chapter 2, in Chapter 3 we focused on examining how this type of dispersal might contribute to passive changes in tree species diversity in Catalonia, an area characterized by a history of land use changes and intense forests exploitation. For such, we used data collected from the second and fourth Spanish National Forest Inventory sampled between 1989-2016. We also accounted for the factors that could influence diversity changes in the area such as bioclimatic conditions, land use history, connectivity, protection, forest management and structure, and changes in temperature and precipitation over the studied period. Moreover, we assessed whether species changes were derived from the local or the regional pool and which specific functional traits were most relevant for diversity changes (i.e., seed dispersal type, shade and drought tolerance,). Our results showed that after ca. 30 years, tree species diversity passively increased in the area for both the tree and regeneration layers. This trend was mediated by land use history, forest management and by temperature and precipitation changes: diversity increase mostly occurred in long-established and non-recently managed forests; while temperature increase and precipitation decrease showed contrasting effects for the tree and the regeneration layer. Ultimately, higher drought tolerant species and especially, those animal dispersed ones arriving from the regional pool mostly drove diversity increase in all forest types, emphasizing their positive role for maintaining diversity under climate change.

In Chapters 2 and 3, we emphasized how biological interactions, such as seed dispersal by animals, are key processes for ecosystem recovery. However, while biological interactions are crucial for successful restoration, current efforts, such as rewilding, also stress the importance of other ecosystem processes such as disturbance stochasticity and connectivity to achieve restoration goals and ensure long-term resilience. As so, in Chapter 4 we conducted a meta-analysis of 42 studies to explore whether rewilding interventions aimed at increasing biodiversity, promoting natural disturbance regimes and connectivity may increase ecosystem resilience to abiotic and biotic disturbances. Our results determined that rewilding interventions generally enhanced resilience of demographic processes, biodiversity, biophysical characteristics and characteristics of a more semi-natural disturbance regime Nonetheless, specific factors such as the resilience approach and dimension addressed, the disturbance agent and the nature of the interventions practiced were observed to play crucial roles in determining the outcomes of rewilding. As such, rewilding proved to be effective for maintaining native plant community when coping with biotic

disturbances (e.g., invasive species). However, less benefits were observed to address socio-ecological resilience and to cope with abiotic disturbances (e.g., drought, fire), suggesting that these may require complementary measures. Moreover, we found a clear underrepresentation of the dispersal component, highlighting a gap in addressing this crucial ecological function for post-disturbance recovery in rewilding efforts.

These findings will enhance our understanding of ecosystem recovery and resilience, particularly in the face of biodiversity loss and increasing climate change disturbances, and they may provide valuable insights for restoration assessments. As nations worldwide work on developing restoration plans, such as the UN Decade on Ecosystem Restoration (2021–2030) and the EU Restoration Law, our results could be important for evaluating and assessing returns on restoration investments, as for improving the quality of future efforts to repair degraded forests in different regions. Yet, our results also raise important questions about whether current restoration strategies aimed at boosting resilience in the face of climate change will be sufficient to address the growing threat of abiotic disturbances, such as extreme wildfires or drought events.

Chapter 1-

General Introduction

1.1. Tackling the twin biodiversity and climate change crises

The world is facing an accelerating dual crisis of biodiversity loss and climate change, which are intricately connected and mutually reinforcing (Bellard et al., 2012). By recognizing the critical role that natural ecosystems play in regulating climate, supporting biodiversity, and providing a myriad of ecosystem services, societies worldwide are increasingly aware of their dependence on these habitats, galvanizing global efforts to reverse their degradation and destruction, and aiming to enhance ecosystem resilience (Pörtner et al., 2023). Facing this urgent necessity, global agreements such as the Convention on Biological Diversity (CBD, 2010), the UN Decade on Ecosystem Restoration (2021–2030) (UN, 2019), or the EU Green deal (EC, 2019) and the Nature Restoration Law (2024), are examples of awareness and driving efforts to protect and rehabilitate natural habitats while simultaneously mitigating climate impacts to face uncertain ecological scenarios.

These initiatives have the enormous potential of enhancing biodiversity, ecosystem functions and services, ecological integrity and connectivity as long as they are efficiently implemented (Gann et al., 2019). Yet, during the development of restoration initiatives, occasional barriers may be encountered, and unsuccessful restoration efforts are noted failing to sustain gains over time owing to political and economic interests, lack of evaluation and monitoring, uncertainty due to increasing disturbance events or unforeseen environmental challenges (Moreno-Mateos et al., 2017) manifesting the critical need to assess the outcome of restoration actions. Despite these obstacles, we are approaching a pivotal moment that offers a unique opportunity to address human-induced and climate change-driven ecosystem degradation and mitigate their negative impacts on biodiversity and ecosystem functions and services. For such, it is essential to identify and understand the drivers of successful restoration (e.g., specific species attributes, environmental conditions, etc.) to provide foundations for developing targeted strategies that address specific challenges and ensure the resilience of restoration efforts over time, specifically under the context of global change (Gann et al., 2019).

1.2. Seed dispersal as a key process in ecological restoration success

Ecological restoration consists of the recovery of an ecosystem that has been degraded, damaged or destroyed which's ultimate goal is to establish self-regulating ecosystems that are resilient to disturbances without further assistance (SER, 2021). But how can we recognize when we have achieved the goal? Evaluating restoration is not straightforward, with extensive debates surrounding what characterizes successful restoration and how it is best to measure (Wortley et al., 2013). Many authors have suggested restoration success to be based on species diversity and abundance (e.g., Reynolds et al., 2012; Shaw, 2019), vegetation characteristics (e.g., Hale et al., 2018; Pittarello et al., 2016) or ecosystem processes (e.g., Herrick et al., 2006; Ribeiro da Silva et al., 2015). However, other authors have proposed more integrated approaches which include more than one of the abovementioned variables together, to offer more accurate measures of restoration success (Ruiz-Jaén & Aide, 2005).

Attempts to evaluate the success in recovering habitats have usually focused on compositional and structural aspects of biodiversity assuming that they can be proxies for inferring the extent of the recovery of ecological processes (Brudvig, 2011; Forup et al., 2008; Young, 2000). Yet, without assessing these processes, we cannot accurately determine if an ecosystem is truly recovering or if it is merely reestablishing surface-level characteristics (Herrick et al., 2006; Ruiz-Jaén & Aide, 2005). Seed dispersal plays a crucial role in maintaining plant populations and ecosystem dynamics and, in many cases, it is the major limiting factor for ecosystem recovery (Holl et al., 2000). This is so because seed dispersal plays a key role in ecosystem restoration, transporting seeds into restoration sites and determining the spatial distribution of plants, facilitating colonization of new areas, and helping maintain genetic diversity within plant populations (Jordano & Godoy, 2002; Silva et al., 2020). Thus, dispersal limitation is an ecological barrier that severely impairs the establishment of plant species in restoration sites, mainly of zoochorous plant species (Holl et al., 2013; Silva et al., 2020). As so, different authors have stated that the recovery of ecological interactions, specifically of plant-seed disperser interactions, is critical for the long-term functioning of restored ecosystems (e.g., Forup et al., 2008; Ribeiro da Silva et al., 2015). Therefore, analyzing the factors that influence seed dispersal mechanisms and its implications for restored sites can serve as a valuable tool for assessing and monitoring the recovery of seed dispersal functions, and by extension, forest restoration success.

Interestingly, in many plant communities, seed dispersal by animals is often the main type of propagule dissemination and thus, it is essential for their long-term maintenance (Forup et al., 2008; Viani et al., 2015). On average, 90% of woody plant species in tropical forests and up to 62% in temperate forest produce fruits that are dispersed by animals (Herrera, 1984; Howe & Smallwood, 1982). Frugivorous birds and mammals ensure seed arrival into available sites, and may show noticeable impacts on plant recruitment and plant distribution patterns (e.g., Fedriani et al., 2018; García-Cervigón et al., 2017) constituting an important element for successful woody recolonization of both natural and human-altered landscapes (Puerta-Piñero et al., 2013). However, the successful arrival of seeds into recolonization sites may depend on many different factors including plant and animal functional traits (e.g., seed size) and behavior of dispersal agents (e.g., scatter-hoarding) (Howe, 2016), environmental factors (e.g., distance from seed sources, landscape structure, etc.) (Carlo et al., 2013) or specific socio-ecological factors (e.g., past land use legacies) (Cruz-Alonso et al., 2021) (Fig. 1.1).

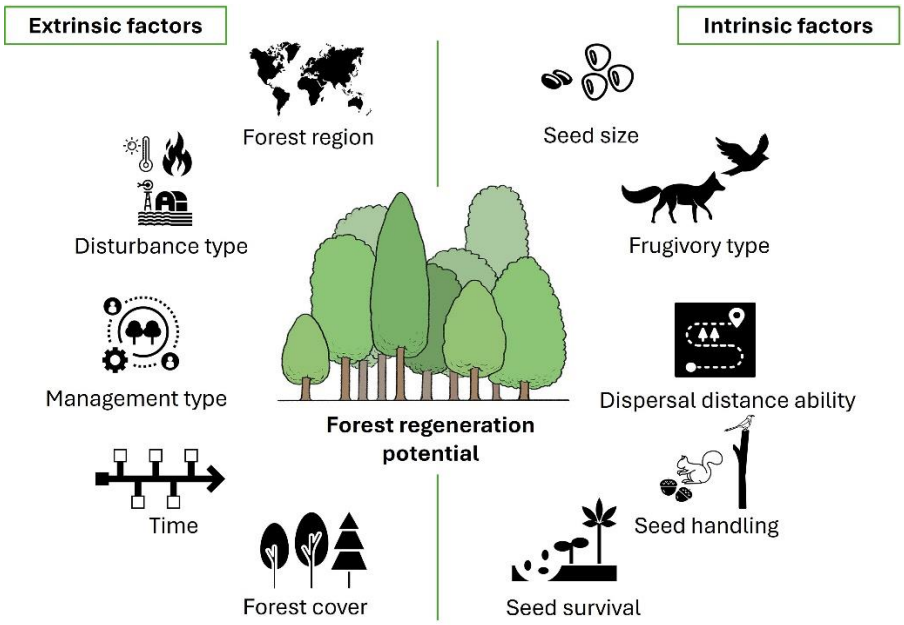


Figure 1.1. Conceptual drawing illustrating different extrinsic and intrinsic dispersal factors influencing forest regeneration potential.

On one side, a large amount of literature has explored the "intrinsic" factors which relate to the dispersal syndromes and disperser traits that predict the mutualistic interactions between fruiting plants and the animals that disperse their seeds (e.g., Fedriani et al., 2018; Howe, 2016; Vander Wall & Beck, 2012; Wenny, 2001). Such factors may ultimately affect the condition of the viable seeds and modulate their ability to reach potential suitable sites for recruitment, including seed size and shape (Vander Wall & Beck, 2012), animal seed dispersal distance ability (Wotton & Kelly, 2012) and animal seed handling methods (Muñoz et al., 2017; Traveset & Verdú, 2002). Moreover, the richness and abundance of plants and dispersal agents may also directly determine the strength of plant-animal interactions, and thus the potential capacity of seeds to reach suitable sites (Naoe et al., 2018). On the other side, "extrinsic factors" which relate to the full environmental context into which the seeds are dispersed will finally determine if they succeed (Wolfe et al., 2019). In this context, several factors such as climatic conditions, amount and proximity of forest cover (i.e., connectivity), microsite availability, and land-use legacies have been identified to affect seed dispersal and seedling establishment (Cruz-Alonso et al., 2021; Vayreda et al., 2013). Interestingly, the effects of intrinsic and extrinsic dispersal factors may potentially differ in different regions (e.g., biomes) which may be subjected to different biotic, abiotic or socio-ecological conditions which shape plant and animal species composition and even, restoration approaches (Ruiz-Jaén & Aide, 2005). Moreover, usually, attempts to evaluate restoration outcomes have generally focused on specific factors at a time or specific forest types (Mittelman et al., 2020; Peña-Domene et al., 2014). Thus, the questions of whether and how intrinsic and extrinsic dispersal factors may affect restoration outcomes remain unaddressed, and thus answering such questions will be important for prioritizing restoration actions.

1.3. Towards more diverse forests in a time of global change

By fostering diverse species compositions, restoration initiatives can better support the long-term stability and adaptability of forest ecosystems, as systems with greater biodiversity are generally considered to better maintain ecosystem functions in the face of disturbances (Jactel et al., 2017; Messier et al., 2022a) that is, exhibiting higher resilience (i.e., the capacity of a system to absorb disturbances and reorganize after environmental change; Folke et al., 2004). Indeed, tree species diversity may play a key role for sustaining forest functioning under increasing disturbance

events (Johnstone et al., 2016) as it increases the range of species responses to disturbances, and provides functional complementarity in the efficient use of resources (the insurance hypothesis; Yachi & Loreau, 1999). Thus, by emphasizing the importance of biodiversity and addressing the underpinning factors posed by both land-use and climate change which may affect diversity changes, restoration efforts can aim to create more resilient ecosystems.

However, the increase in tree species diversity may be challenging as some authors have indicated it could require long periods of time due to complex ecological and environmental dynamics (Bauhus et al., 2017). As so, different environmental factors influencing propagule availability include changes in climatic conditions (García-Valdés et al., 2015), land use legacies (Cruz-Alonso et al., 2021), past and recent management (Chaudhary et al., 2016), forest protection (Lecina-Diaz et al., 2019) and forest structure and connectivity (Crowther et al., 2015) (Fig. 1.2). Regarding climatic conditions, temperature and precipitation are critical factors affecting seedling recruitment, influencing germination, growth and survival (Corlett & Westcott, 2013). Seedling recruitment is influenced by the interplay of the adaptations of each species to local climate, and thus, understanding these local dynamics helps in predicting plant responses to environmental changes (Craine & Dybzinski, 2013). However, increasing changes in climatic patterns can alter the availability and timing of temperatures and precipitation (e.g., increasing temperatures and severe drought periods), creating mismatches in the conditions required for successful seedling recruitment, and potentially leading to shifts in plant community composition (Corlett & Westcott, 2013; Sánchez de Dios et al., 2023; Vayreda et al., 2013). Interestingly, a notable trend to passive afforestation has emerged in many regions in recent decades due to the abandonment of agricultural land. This phenomenon is particularly evident in certain parts of Europe (e.g., Mediterranean), where socioeconomic changes have led to the decline of traditional practices (Palmero-Iniesta et al., 2020). Such reversion of land has led to the natural succession of abandoned fields, creating corridors that link forest fragments, facilitating the movement of wildlife and the dispersal of plant species, and ultimately may increase biodiversity (Frei et al., 2024). Such improved connectivity may play a pivotal role in seed dispersal, which finally can determine which species and in what abundance are found in an area by facilitating the movement of dispersal agents across the landscape (Holl et al., 2013; Silva et al., 2020).

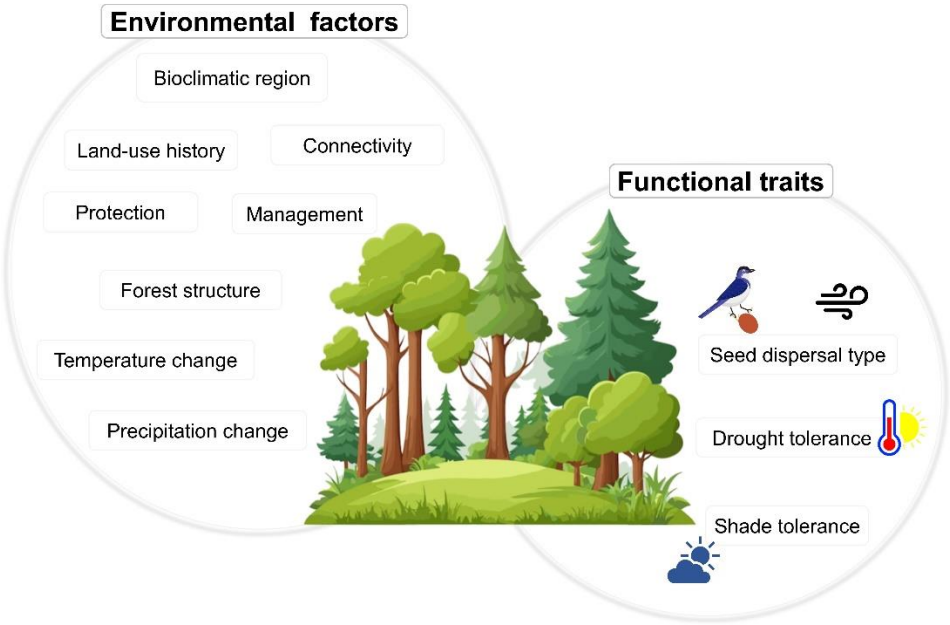


Figure 1.2. Main environmental factors and species functional traits that may affect tree species diversity changes over time.

Thus, identifying the functional traits of the species involved is also essential as they determine the ability of species to overpass ecological filters and finally contribute to potential complementary effects (Craine & Dybzinski, 2013). Seed dispersal type (i.e., animal mediated seed dispersal *vs.* other methods such as wind) is a key factor filtering species presence and abundance at community and landscape levels (Forup et al., 2008; Viani et al., 2015) (Fig. 1.2). However, to fully assess the potential success of tree species recruitment after dispersal, it is crucial to also consider other functional traits that impact environmental filtering such as drought and shade tolerance as it will determine the ability of recruits to establish and survive under limiting water availability and to thrive in low-light environments, such as under the canopy of other plants (Holmgren et al., 2012) (Fig. 1.2). Moreover, as land conversion are set to continue (Foley et al., 2005), it is crucial to understand how these changes, along with other environmental factors and species functional traits, may impact biodiversity. Although the importance of biodiversity is widely recognized (Jactel et al., 2017; Messier et al., 2022a), few studies have examined long-term changes in tree species diversity while considering together environmental factors and species traits and nevertheless, have explored whether such diversity changes arise from local forest

dynamics (e.g. ingrowth of seedlings into the tree layer) or from the dispersal and recruitment of species from the regional pool. Such understanding will be essential for predicting future biodiversity shifts and it will be especially important in the context of climate change, where water availability and light conditions are increasingly variable (Barnagaud et al., 2013; Johnstone et al., 2016).

1.4. Integrating resilience into novel restoration approaches: The case of rewilding

Even if restoration projects achieve their initial success, they may struggle to sustain their gains over time due to the threats posed by shifting climatic conditions (e.g., temperature and precipitation changes) and increasing intensity and recurrence of natural disturbances (e.g., extreme weather events, invasive species) (e.g., Ballari et al., 2019; Cava et al., 2018; Travers et al., 2021). Consequently, there is an increasing need to review and assess the resilience of restoration efforts within new ecological scenarios characterized by heightened uncertainty and more frequent disturbances (Donohue et al., 2016; Svenning, 2020). This evaluation must be more comprehensive considering a more diverse set of factors, including biodiversity recovery, ecological processes, and holistic management strategies, to ensure long-term ecological stability (Messier et al., 2022a; O'Connor et al., 2020). As stated in the previous sections, trophic interactions (e.g., frugivory) together with the dispersal capacity of organisms are crucial ecological process that enable the movement and colonization across various landscapes, facilitating recovery after disturbances (Leimu et al., 2006; Vranckx et al., 2012). While dispersal and trophic complexity are often prioritized in ecological restoration efforts (Solé & Montoya, 2001), the role of natural disturbances is typically overlooked (Franklin et al., 2000). However, ensuring long-term ecological stability and resilience requires considering all these critical processes including natural disturbance regimes (Franklin et al., 2000). In these lines, "rewilding" is gaining momentum in the scientific community as a promising approach to ecological restoration that aims to recover such ecological processes with the aim of promoting complex, self-regulating ecosystems while reducing human intervention (Perino et al., 2019; Torres et al., 2018).

Thus, rewilding has evolved from its initial conceptualization which highlighted the regulatory role of large predators as keystone species, essential for preserving the diversity and resilience of

ecosystems through top-down trophic control (Soulé & Noss, 1998), to encompass a variety of diverse, process-oriented, and dynamic approaches aimed at restoring biodiversity (Fernandez et al., 2017) and contributing to ecosystem resilience (Jarvie & Svenning, 2018; Svenning, 2020). In these lines, Perino et al. (2019) proposes that ecosystem complexity and resilience are maintained by the interactions among three critical components of natural ecosystem dynamics, namely trophic complexity, stochastic disturbances, and dispersal or connectivity (Fig. 1.3).

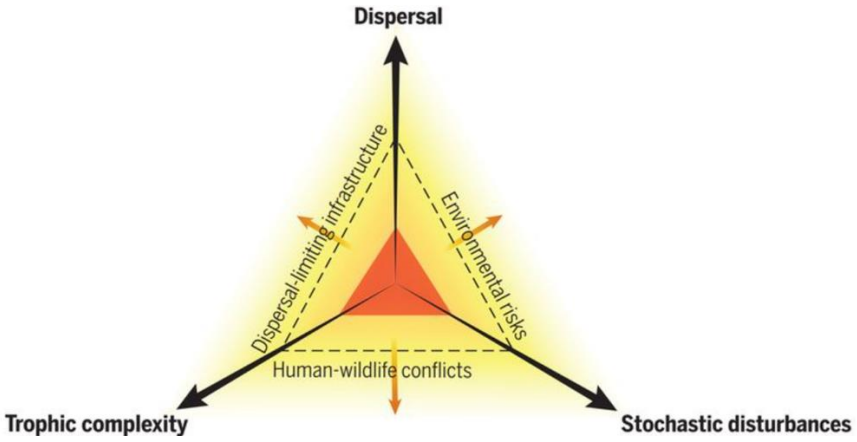


Figure 1.3. Rewilding can be assessed by representing the state of the ecosystem in a three-dimensional space where each dimension corresponds to an ecological process. The difference in volume between the restored (yellow pyramid) and the degraded ecosystem (orange pyramid) is a proxy for the effects of rewilding on the self-sustainability of the ecosystem. Modified from Perino et al. (2019).

Overall, trophic complexity may contribute to more self-sustaining and resilient ecosystems by fostering biodiversity, stabilizing population dynamics through trophic interactions, enhancing nutrient cycling and energy flows (Foster et al., 2014). Ultimately, these processes increase resilience by buffering ecosystems against disturbances through providing functional complementarity and increasing ecosystem adaptability (Solé & Montoya, 2001). Additionally, natural disturbances are often suppressed or altered in their magnitude and frequency (e.g., fire suppression, flooding control, etc.) especially in human-dominated landscapes, leading paradoxically to more devastating disturbance events (e.g., large wildfires instead of smaller and

more frequent ones) (Bengtsson et al., 2021). Instead, disturbances which occur in a more stochastic manner are critical drivers of spatial and temporal heterogeneity in ecosystems and may trigger their reorganization leading to increased ecosystem complexity (Franklin et al., 2000). They promote coexistence between species and may increase the ecosystem resilience to disturbance events such as floods, invasive species, pest outbreaks, or fires favoring a higher resistance or promoting recovery and reorganization (Bengtsson et al., 2021). Finally, a reduction in dispersal between populations can cause them to become increasingly affected by the effects of genetic drift and reduced gene flow, resulting in fitness and genetic diversity loss, leading populations to become less resilient to environmental and demographic changes and more likely to go extinct (Leimu et al., 2006; Vranckx et al., 2012). It can also lead to population decline, with a lower chance of populations being rescued or suitable patches being colonized resulting in biodiversity losses (Ibáñez et al., 2014). Moreover, dispersal is also required for organisms to migrate successfully to more suitable climates in response to climate change (Corlett & Westcott, 2013). Thus, the exchange of individuals from different populations can increase gene flow, mitigate inbreeding, and hence lead to more viable populations.

Consequently, rewilding interventions aimed at restoring the three components defined by Perino et al. (2019) (i.e., trophic complexity, stochastic disturbances and dispersal) can be identified as a key process to increase resilience. Yet to date, there have been seldom efforts to assess resilience in rewilding projects probably due to the to the multiple interpretations of resilience (i.e., different approaches, multiple dimensions and metrics, precise timescales), the intricate and dynamic nature of ecosystems and the diverse types of disturbances they face. However, recent proposals have emerged to develop conceptual frameworks for quantitatively assessing and applying resilience. Among these frameworks the "Operational Resilience Framework (ORF)" developed by Lloret et al. (2024), provides a unified terminology and a sequence of steps to assess resilience (Fig. 1.4). The ORF focuses on recognizing and relating several elements, including: the resilience approach (i.e., engineering, ecological, socio-ecological), the system variables addressed (i.e., *resilience of what* sensu Carpenter et al. (2001), and the type of disturbances and stressors acting at given spatiotemporal scales (*resilience to what* sensu Carpenter et al. (2001) (see Lloret et al. (2024) for a more extensive description of these elements). Thus, by identifying variables (i.e., resilience predictors) suitable to be managed to enhance the resilience of the system, the ORF helps to improve the understanding of how to strengthen ecosystems against disruptions. Ultimately, by

integrating the latest frameworks for assessing rewilding with those developed for measuring resilience, the benefits of this novel restoration strategy in addressing increasing climatic uncertainties can be better evaluated.

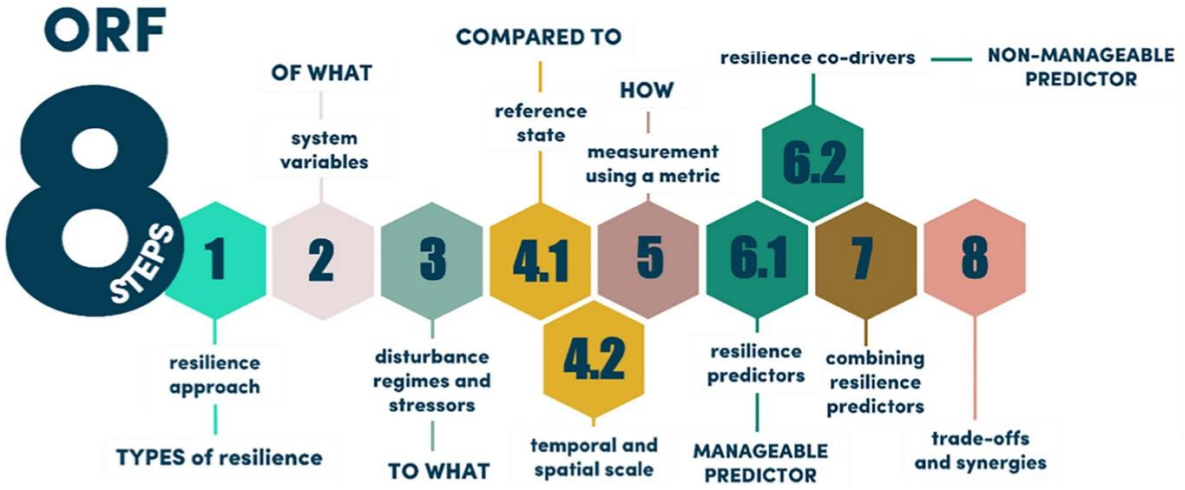


Figure 1.4. Roadmap of the eight steps for applying the operational resilience framework (ORF) to assess resilience in specific case studies. Modified from Lloret et al. (2024).

1.5. Objectives

By specifically focusing on the role that animal mediated seed dispersal plays for restoration success in forest ecosystems, this thesis investigates the interactions between different abiotic (e.g., climatic) and biotic (e.g., functional traits) factors which may influence changes in tree species diversity. Moreover, we aim to explore whether the novel perspective of the "rewilding" concept for restoration can enhance resilience to cope with the challenges posed by climate change and related disturbances.

More precisely, in this thesis we aimed at addressing the following questions: (Q1) which is the relative contribution of intrinsic and extrinsic factors influencing animal-seed dispersal for forest restoration success across biomes? (Chapter 2); (Q2) which are the different environmental and forest management factors triggering passive changes in tree species diversity and which functional traits (e.g. dispersal method, shade and drought tolerance) modulate the ability of tree

species to surmount ecological filters shaping recruitment success? (Chapter 3); and (Q3) Do interventions targeting rewilding components (i.e., trophic complexity, stochastic disturbances, and dispersal) increase resilience under climate change disturbances? (Chapter 4). The specific objectives for each chapter are listed below:

Chapter 2: In this chapter we aimed to assess the role that animal-seed dispersal plays in forest restoration efforts worldwide, and independently for tropical and temperate biomes, where most plants depend on this type of dispersal. For such, we conducted a systematic review and determined which intrinsic factors related with the dispersal syndromes and traits (e.g., seed size, seed handling methods) and extrinsic (e.g., forest cover, microenvironmental conditions) were assessed in the primary studies, and then we evaluated their importance for the success in the restoration outcome. Particularly, we addressed two main questions: (i) which is the relative contribution of intrinsic and extrinsic factors influencing animal-seed dispersal for forest restoration success? and (ii) does the importance of such factors differ among forest regions (i.e., tropical vs. temperate biomes) in their restoration outcome?

Chapter 3: In this study we aimed to analyze to what extent species functional traits (e.g., dispersal type, shade and drought tolerance), forest management (e.g., logging, protection), and environmental factors (e.g., temperature and precipitation) have influenced passive changes in tree species diversity at a regional scale (i.e., Catalonia, NE Spain). Specifically, we investigated the role of tree species functional traits and their interaction with the bioclimatic region, land use legacies, forest cover, forest protection, past and recent management, forest structure and changes in temperature and precipitation during the period between 1986-2016 to account for changes in species diversity in the tree and regeneration layers by using the data derived from the second (1989) and fourth (2016) Spanish National Forest Inventory. We also explored whether diversity changes were driven by local dynamics (i.e. ingrowth and local regeneration) or by the arrival of new species from the regional pool. Particularly, we addressed three main questions: (i) has tree species diversity passively changed over the studied period? (iii) which functional traits (i.e. dispersal method, shade and drought tolerance) have most contributed to these changes? (ii) were changes in tree species diversity mostly driven by local dynamics or by the arrival of species from nearby?

Chapter 4: in this chapter we aimed to understand whether, and by which mechanisms rewilding practices may increase ecosystem resilience under increasing climate change related disturbances. We followed a meta-analytical approach which coupled the theoretical framework for rewilding targets proposed by Perino et al. (2019) and the operational resilience framework (ORF) developed by Lloret et al. (2024). Our approach allowed us to assess the role of the three rewilding components (i.e., trophic complexity, disturbance stochasticity and dispersal) proposed by Perino et al. (2019) as resilience predictors (i.e., manageable characteristics that increase resilience) according to the ORF framework developed by Lloret et al. (2024) in response to disturbances. Particularly, our research aimed to: (i) analyze and describe the available scientific literature assessing empirical measures of resilience in rewilding projects, (ii) evaluate the suitability of different rewilding interventions aiming at the increase of trophic complexity, stochastic disturbances and dispersal for the increase in ecosystem resilience, and more specifically (iii) explore the potential impact of different rewilding interventions aimed at increasing trophic complexity for ecosystem resilience.

Finally, in **Chapter 5** we discuss the main results of this thesis and suggest further topics to be investigated

Chapter 2 -

Disentangling the importance of intrinsic and extrinsic seed dispersal factors in forest restoration success: a global review

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2.1. Abstract

Animal-mediated seed dispersal is envisaged as a key process to promote forest restoration success. Yet, we lack a comprehensive knowledge of the contribution of intrinsic and extrinsic factors which directly and indirectly influence this process and, ultimately, restoration outcomes. Here, we reviewed 157 articles to identify the most relevant intrinsic (e.g., plant and animal species traits) and extrinsic (e.g., connectivity) factors which mediate the seed dispersal process. We analyzed the contribution of such factors to restoration success, as identified in the reviewed articles, globally and for tropical and temperate biomes. Generally, our analysis revealed that the main factors affecting restoration success were the extrinsic ones (i.e., connectivity, type of restoration conducted, forest protection and disturbance degree), while the ability of animals to achieve long distance dispersal was the main intrinsic factor. Differences among biomes were observed for extrinsic factors, specifically for restoration approach, as more intense efforts seem to be needed for successful restoration in tropical systems (i.e., reconstructive restoration), whereas assisted restoration (e.g., perch placements) was mostly enough for temperate ones. Within intrinsic factors, rodent frugivory and "large-sized" seeds were related to unsuccessful restoration in tropical forests, while frugivory by carnivores and "small-sized" seeds favored restoration in temperate ones, and the main constraint to success in this biome was ungulate frugivory. Our results highlight the importance of distinguishing between intrinsic and extrinsic factors mediating animal seed dispersal in forest restoration in different biomes. Furthermore, this paper will help to promote adequate measures when planning restoration actions.

Keywords: active and passive restoration, frugivory, functional restoration, plant-animal interactions, tropical and temperate forests.

2.2. Introduction

Habitat destruction and land use changes over the past centuries have contributed to the loss and fragmentation of landscapes that show a substantial impact on habitat structure and biodiversity, leading to severe ecological disruptions and to the loss of important ecosystem processes and services (Bello et al. 2015; Kurten 2013). Society's current awareness of its dependence on forests has become a major global concern, underpinning international initiatives to reverse degradation and destruction of forest ecosystems worldwide (e.g., United Nations Decade on Ecosystem Restoration (2021-2030), Aichi Biodiversity Targets, E.U. Forest Strategy, E.U. Green Deal) (Aronson et al. 2020; Crouzeilles et al. 2016; Meli et al. 2017). Although a critical need to assess the outcomes of forest restoration actions has been repeatedly claimed, the global forest restoration community still lacks a comprehensive review for the evaluation and verification of the efficacy of such initiatives (FAO 2020).

Evaluating restoration is not straightforward, with extensive debates surrounding what characterizes successful restoration and how it is best to measure (Wortley et al. 2013). Usually, attempts to evaluate the success in recovering disturbed habitats have focused on compositional and structural aspects of biodiversity such as species richness and abundance (Brudvig 2011; Forup et al. 2008; Ruiz-Jaen & Aide 2005) assuming that they can be proxies for inferring the extent of the recovery of ecological functions (Majer & Nichols 1998; Young 2000). Following the basic guidelines for restoration planning provided by SER (2021), three general attributes (i.e., vegetation structure, species diversity and abundance, and ecological processes) have been proposed to help practitioners identify appropriate indicators for restoration success (Ruiz-Jaen & Aide 2005). Thus, an alternative is to evaluate the re-establishment of complex ecological interactions and the ecological functions that they provide as the starting point for rebuilding community structure (Forup et al. 2008; Ribeiro da Silva et al. 2015). One of such functions is seed dispersal, which may play a key role in ecosystem restoration, transporting seeds into disturbed sites and linking the end of the reproductive cycle of source adult plants and their subsequent life cycle stages (Bakker et al. 1996; Forget et al. 2011; Jordano & Godoy 2002). Within seed dispersal mechanisms, we chose to focus on animal-mediated seed dispersal, provided by the interactions between fruiting plants and frugivorous animals (Forget et al. 2011; Jordano & Godoy 2002). This dispersal type has been acknowledged to largely influence plant distribution

patterns by facilitating the establishment of seeds in new habitats away from the mother plant (Rubalcava-Castillo et al. 2021; Traveset et al. 2007). Moreover, in many plant communities, seed dispersal by animals is often the main form of dissemination of propagules and thus, essential for the long-term maintenance of forests where most plant species rely on this mechanism rather than wind, water, or other forms of dispersal (Forup et al. 2008; Rubalcava-Castillo et al. 2021; Viani et al. 2015). For example, on average, 90% of woody plant species in tropical forests and up to 62% of temperate forest species produce fruits that are dispersed by animals, usually birds and mammals (Herrera 1984; Howe & Smallwood 1982).

Analyzing the factors affecting seed arrival and survival in restored forests can provide a useful tool for evaluating and monitoring the recovery of seed dispersal functions and thus, forest restoration (Tylianakis et al. 2010). On the one hand, seed dispersal can be directly affected by several "intrinsic" factors, which relate to the traits of the dispersed plants and their dispersal agents (e.g., species life-history traits, animal behavior) as well as species richness and abundance (Schupp et al. 2019). These intrinsic factors include fruit handling methods (e.g., legitimate seed dispersal by animals that swallow entire seeds and defecate or regurgitate them in viable conditions for germination, *sensu* Traveset 1994, seed predation, scatter hoarding), animal seed dispersal distance ability and plant dispersal traits (e.g., seed size, amount of fruit reward) (Baños-Villalba et al. 2017; Li et al. 2019). In addition, the richness and abundance of the dispersed plants and dispersal agents have been considered as intrinsic factors as they will also directly determine the strength of this plant-animal interaction and thus, the capacity of seeds to reach restoration sites (Kuprewicz 2013; Naoe et al. 2018; Orrock et al. 2006). On the other hand, "extrinsic" factors have been defined as those indirect factors that may (or may not) affect animal seed dispersal, and ultimately restoration success through their potential effects on the disperser community composition and behavior (Molin et al. 2018; Wolfe et al. 2019). These extrinsic factors are related to the environment, including the amount and proximity of forest cover (i.e., connectivity), micro-site availability, conditions for seed deposition and climatic constraints. Other extrinsic factors may be related to human intervention, such as past land use type, restoration approach (i.e., passive vs. active) and context (e.g., disturbance degree (i.e., initial conditions of the study sites)), time since restoration and forest protection, which can also influence restoration success (Crouzeilles et al. 2016; Koelemeijer et al. 2021; Molin et al. 2018).

Finally, the effects of intrinsic and extrinsic dispersal factors in determining restoration success may potentially differ across biomes, as they are subjected to different biotic, abiotic and socioeconomic conditions which shape fauna and flora composition, land use and management types and, even, restoration approaches (Aide et al. 2013; Clark et al. 1999). Regarding intrinsic factors, differences may relate to dispersal agents' composition, animal seed dispersal distance ability or seed size (Hanya & Aiba 2010). While for extrinsic factors it would be likely to *a priori* assume similar effects within biome types, yet it cannot be discarded that differences may arise from the actions performed (i.e., type of disturbance, forest protection, restoration approach) which would ultimately affect restoration success.

Thus, a global analysis of forest restoration outcomes determined by intrinsic and extrinsic dispersal factors, which to our knowledge, have seldom been surveyed simultaneously, is appropriate given that most case studies have mostly focused on specific forest types (de la Peña-Domene et al. 2014; Mittelman et al. 2020).

Here, we conducted a literature review to assess the role of animal-mediated seed dispersal in forest restoration efforts worldwide, and independently for tropical and temperate biomes. Specifically, we determined which intrinsic and extrinsic factors were assessed in the restoration studies reviewed and then, we evaluated their importance for the outcome of restoration globally and across biomes. To this end, we addressed two main questions: (1) which is the relative contribution of intrinsic and extrinsic dispersal factors in forest restoration success? and (2) does the importance of such factors in the restoration outcome differ among forest regions (i.e., tropical vs. temperate biomes)? The answers will be important for prioritizing restoration actions and for their smart design in the recovery of different ecosystem types.

2.3. Materials and Methods

Literature search

We searched for published studies of forest restoration that focused on seed dispersal functions as a key ecological process towards ecosystem restoration. For this review we followed Pickering & Byrne's (2014) recommendations for systematic quantitative approaches to literature reviews, and

Romanelli et al. (2021) for repeatability of reviews of restoration outcomes. Two global databases were selected to carry out our literature search: Web of Science and Science Direct. For both databases we searched for the following combination of words in the title, abstract or keywords: seed dispersal AND (forest OR ecosystem OR ecological) AND (restoration OR recovery OR regeneration). The search was limited to the above-mentioned terms to target papers not only focusing on active restoration strategies (i.e., restoration, recovery) but also passive (i.e., regeneration). We chose to include the aforesaid terms rather than others such as "rehabilitation" to be more consistent with the terms provided in the SER definition of ecological restoration (SER 2021). We also chose to include "forest" rather than "woodland" or "timberland" as our experience with the literature and keywords search showed that most papers that use these other terms also included "forest" and would be acquired by the above search. We obtained 600 articles matching the selected keywords. Then, we excluded all publications that did not describe forest restoration processes by means of seed-dispersal interactions. More precisely, this scrutiny met the following established criteria: (1) the main objective of the study was the assessment of seed dispersal functions in disturbed landscapes affected either by active or passive restoration, (2) the study included a comparison to either a reference ecosystem (forest similar to the project site but non-degraded) or control (degraded forest without restoration treatments) used for the definition of restoration success (see definition below), and (3) the articles included information of the specific intrinsic and extrinsic dispersal factors used for the assessment of the restoration success (see next section). We obtained 157 articles published between 1996 and 2021 which matched the abovementioned criteria. When the same article presented results from two or more study locations that were sufficiently distant (e.g., different continents) and subjected to clearly differentiated conditions (e.g., biome type), the results of each site were considered as independent cases, resulting in a total of 161 items. Thus, the database compiled for this study is new and based on the literature search conducted specifically for this study. The greatest number of works were conducted in tropical and subtropical forests (N = 94 and 23 respectively), while temperate and mediterranean-type climate forests accounted for 22 and 17 publications, respectively. We found 3 assessments in steppe forests and one in savanna and desert forests. Publications were found in studies conducted in 40 countries and the ones with higher number of publications were Brazil (N=35), Spain (N=16), Mexico (N=13) and China (N=12) (See Appendix 1 Supplement S1).

Rationale for parameters and categories used in classification

The information recorded was obtained from each primary study and was classified into general information and intrinsic and extrinsic dispersal factors involved in the restoration process (See Appendix 1 Supplement S2 for detailed description of the database and how it was compiled). General information included full reference details, study period, region, country, continent, patch size (ha) and biome type. As biome information was not standardized across papers, we classified the study cases for climate based on the geographic position of the study site using the global Köppen-Geiger climate classification map (http://koeppen-geiger.vu-wien.ac.at/present.htm).

Intrinsic dispersal factors were considered those related to the attributes of the dispersed plants and their dispersal agents which directly affect the outcomes of seed arrival and survival, while extrinsic factors were those related to habitat conditions or restoration approaches which could indirectly affect the seed dispersal process and thus, forest restoration success (see Fig. 2.1 and Appendix 1 Table S1 for full variable list and descriptions). The qualitative attributes used for intrinsic and extrinsic dispersal factors' classification were based on the description and terms provided in the articles selected for the review. A total of 27 indicators (15 intrinsic, 12 extrinsic) were selected to evaluate their effects on the restoration outcome (Appendix 1 Table S1).

Within extrinsic factors, restoration approaches were classified into (1) "passive", when after cessation of the disturbance, natural (i.e., spontaneous) regeneration proceeds (Gann et al. 2019); or (2) "active", when the potential regeneration is mediated by human intervention. Active restoration was further categorized into: (i) "assisted regeneration", when interventions harness the regeneration capacity of the remaining biota (e.g., removal of alien species) or they aim to reintroduce species that cannot migrate into restoration sites without assistance by, for instance, installing resources to prompt colonization (e.g., perches), or (ii) "reconstruction", when major proportions of biota are introduced (e.g., reintroduction of early successional species) (Gann et al. 2019). When possible, for each factor's category, the exact terms provided in the reviewed articles were used (e.g., disturbance category: "deforestation", "fragmentation", "defaunation"). But for uniformity, some variables were converted into simpler ones, based on the information compiled from each study (e.g., for seed size: "large", "medium", "small"; for animal seed dispersal distance ability: "long", "medium", "short"; for forest cover: "continuous", frequent", "fragmented"; see Appendix 1 Supplement S2). Similarly, categories represented by factors limiting or favoring seed

dispersal and survival (e.g., distance to reference forest) were binary classified as one (1) indicating a limitation on dispersal, or zero (0) indicating no limitation (see Appendix 1 Supplement S2). Finally, for the purpose of this study, and although there is extensive debate on what defines restoration success (Wortley et al. 2013), the degree of forest restoration success (i.e., "high", "medium", "low" or "unsuccessful") was established according to the judgment reported by the authors of each publication on the level of recovery of the ecological characteristics addressed in the particular study (e.g., vegetation structure, species diversity and abundance or ecosystem functioning) (Ruiz-Jaen & Aide 2005). From the four categories of restoration success identified in the primary studies, we then constructed a binary response variable which accounted for those studies that comprised "high" or "medium" ("YES") and "low" or "unsuccessful" ("NO") restoration success to increase the robustness of our further analysis (Cutler et al. 2007). See Appendix 1 Supplement S2 for a more detailed rationale of the classification of forest restoration success.

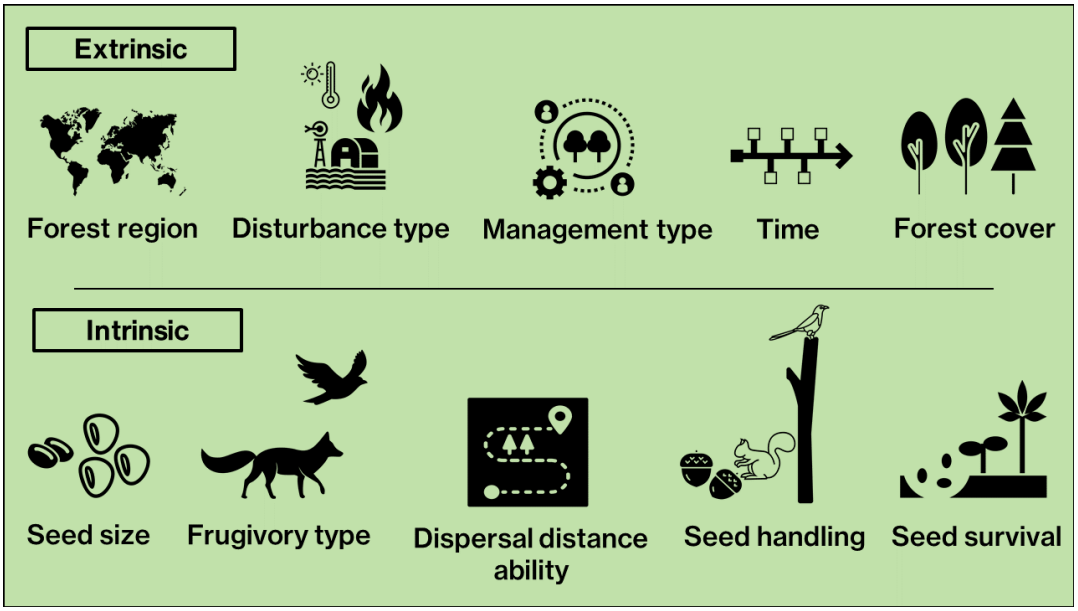


Figure 2.1. Main intrinsic and extrinsic dispersal factors used to evaluate forest restoration success by means of animal-mediated seed dispersal. See Appendix 1 Supplement S2 for complete list of variables and descriptions.

Data analysis

The data analysis was divided into two steps; the first one to characterize the dataset and the second one to investigate which intrinsic and extrinsic dispersal factors promote restoration success globally and individually for tropical and temperate biomes. Accordingly, to characterize the dataset, we first evaluated the distribution of case studies by continent and type of biome, the progression of publications over time, the percentage of cases within each type of disturbance category and the main intrinsic and extrinsic factors used to assess restoration success in each case study. Secondly, to investigate how intrinsic and extrinsic dispersal factors may drive restoration success, we conducted two complementary analyses. Firstly, Two-way Correspondence Analyses (CA) were performed to explore the association between the restoration outcome and the intrinsic and extrinsic dispersal factors identified. For this test, quality of representation tests (measured by the square cosine, Cos2) were carried out to measure the degree of association between the variables and a particular axis (i.e., how good the representation of the variables on each component is) and variable contribution tests (measured by Contrib function) were performed to filter the most representative variables involved in the success of the restoration process (Husson et al. 2016). Secondly, Classification Tree Analyses (CTA) were performed as complementary analysis to further explore the associations obtained in the previous CA. For the CTA tests, class proportions allowed us to explore the relation between the predictor intrinsic and extrinsic dispersal variables, inferring which ones were more relevant in the overall probability of restoration success (Therneau et al. 2015). The CTA tests were built by the rule of binary partitioning in respect of the broader category of restoration success ("YES/NO") response variable (see above). Finally, the Gini Index was used to split and optimize the nodes and to perform quality of representation tests, which indicate how accurate the CTA classification was performed (Cutler et al. 2007).

The above-mentioned analyses were conducted globally. Yet, to detect differences between the most studied biomes, they were separately carried out for tropical and subtropical (hereafter tropical), and temperate and mediterranean (hereafter temperate) systems following The Köppen Climate Classification. All analyses were performed using free software RStudio (v. 1.4.1106) and packages within: dplyr (Mailund 2019), tidyverse (Wickham et al. 2017), rpart (Therneau et al. 2015) and FactoMineR (Husson et al. 2016).

2.4. Results

Characterization of the dataset

Worldwide, few works were published between 1996 and 2005 (N=26) regarding forest restoration by means of seed dispersal; however, published works increased considerably between 2006 and 2021 (N=135). This trend showed some differences between published works for tropical and temperate biomes: the former was present since 1995 and accounted for a total number of 117 case studies until nowadays, whereas publications for the later mostly begun in 2002 and accounted for a total number of 39 case studies (See Appendix 1 Supplement S3). The disturbance categories which caused forest degradation and decline prior to the restoration efforts showed that 99% of the case studies held forest fragmentation, 87% were previously deforested and 28% were defaunated. This scenario was mainly due to nine types of disturbance categories, being agricultural practices, the presence of alien species, inappropriate grazing and pasture lands, and game the most frequent ones (See Appendix 1 Supplement S3).

Regardless of the type of biome, extrinsic factors were slightly more addressed in the reviewed articles (Appendix 1 Supplement S3, Table S2). Moreover, all extrinsic factors were similarly used aside from micro-environmental conditions and game. Contrarily, among intrinsic dispersal factors, disperser richness, animal seed dispersal distance ability, seed size and number of seeds dispersed were the most addressed variables (Appendix 1 Supplement S3, Table S2).

Drivers of restoration success

Globally, the Two-way Correspondence Analysis explained 92.6% of the cumulative variance (X^2 = 536.90, $P = 2.62 \times 10^{-20}$) in the patterns of restoration success, including all intrinsic and extrinsic dispersal factors. The Cos2 quality of representation test showed that most variables were highly represented by these two dimensions (Appendix 1 Supplement S4A). Extrinsic factors which contributed the most to the definition of dimensions and that were associated to a "high" and "medium" restoration success were, in decreasing order of contribution: time since restoration was initiated, "frequent" forest cover, "improvement" of micro-environmental conditions, proximity to the reference habitat, not been subjected to seed attacks (e.g., fungi or infestations), "least degraded" sites and protected forest status. Within intrinsic dispersal factors, animal and plant abundance and richness and "long-distance" dispersal ability contributed the most to restoration

success (Fig. 2.2, Appendix 1 Supplement S4B). Contrarily, frugivory by rodents contributed to "unsuccessful" restoration efforts (Fig. 2.2, Appendix 1 Supplement S4B).

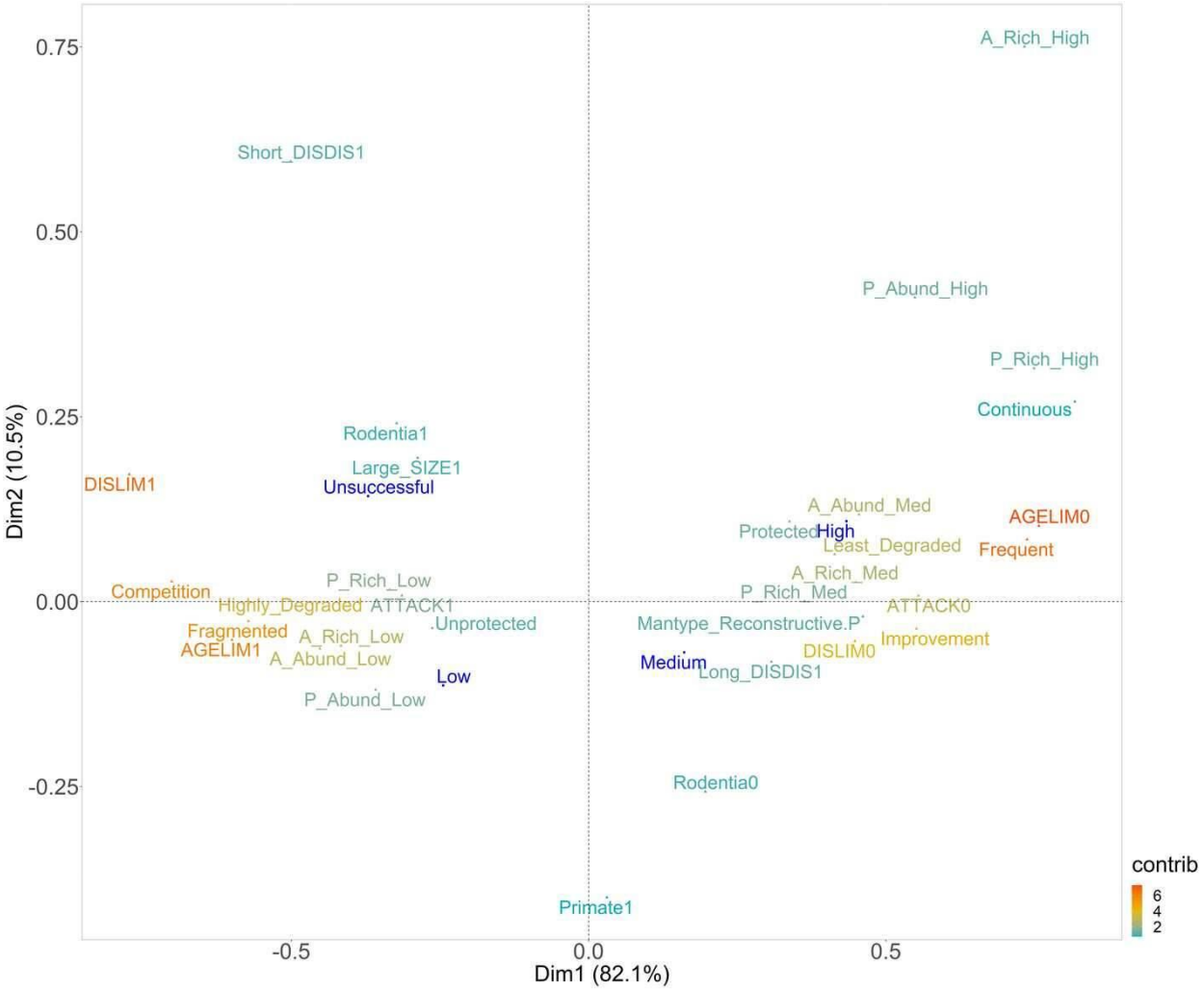


Figure 2.2. Variable contribution for "high", "medium", "low", and "unsuccessful" restoration success (blue labels) in all biomes, defined by two-way Correspondence Analysis. (See Appendix 1 Supplement S2 and Table S1 for variable codes and descriptions). Note that only the 32 variables with the highest contribution are shown.

For the Two-way Correspondence Analysis of tropical (Cumulative % of var. = 88.7, $X^2 = 448.63$, $P = 9.77 \times 10^{-12}$) and temperate systems (Cumulative % of var. = 84.6, $X^2 = 203.40$, $P = 0.98$), most variables were also highly represented by the first two dimensions (Figs. 2.3, 2.4; Appendix 1 Supplement S4C, D). For both tropical and temperate biomes (Figs. 2.3, 2.4; Appendix 1 Supplement S4E, F), extrinsic factors which contributed the most to the definition of dimensions and that were associated with a "high" and "medium" restoration success were, in decreasing order of contribution: higher restoration age, short distance to reference habitat, "improvement" micro-environmental conditions, "frequent" forest cover, and "least degraded" sites. In addition, two other extrinsic factors were further associated to restoration success in tropical systems: absence of seed attacks and reconstructive restoration approach (Fig. 2.3). For temperate systems, specific extrinsic factors that contributed to successful restoration were protected forests and assisted restoration approach, while passive restoration approach contributed to unsuccessful restoration (Fig. 2.4). Intrinsic dispersal factors contributing to both tropical and temperate restoration success were "higher" animal and plant abundance and richness, whereas "long-distance" dispersal ability contributed to tropical forests and carnivorous and "small-medium" sized seeds were more relevant for temperate ones (Figs. 2.3, 2.4). Within the variables which contributed the most to a "low" and "unsuccessful" restoration, we found few differences between biome types (Figs. 2.3, 2.4). For instance, for tropical biomes, the extrinsic factor that was mostly associated to "unsuccessful" restoration was climatic constraints, while intrinsic factors were "large-sized" seeds and rodent frugivory (Fig. 2.3). For temperate biomes, extrinsic factors related to "unsuccessful" restoration were game and passive restoration approach, while ungulate frugivory was the main intrinsic factor (Fig. 2.4).

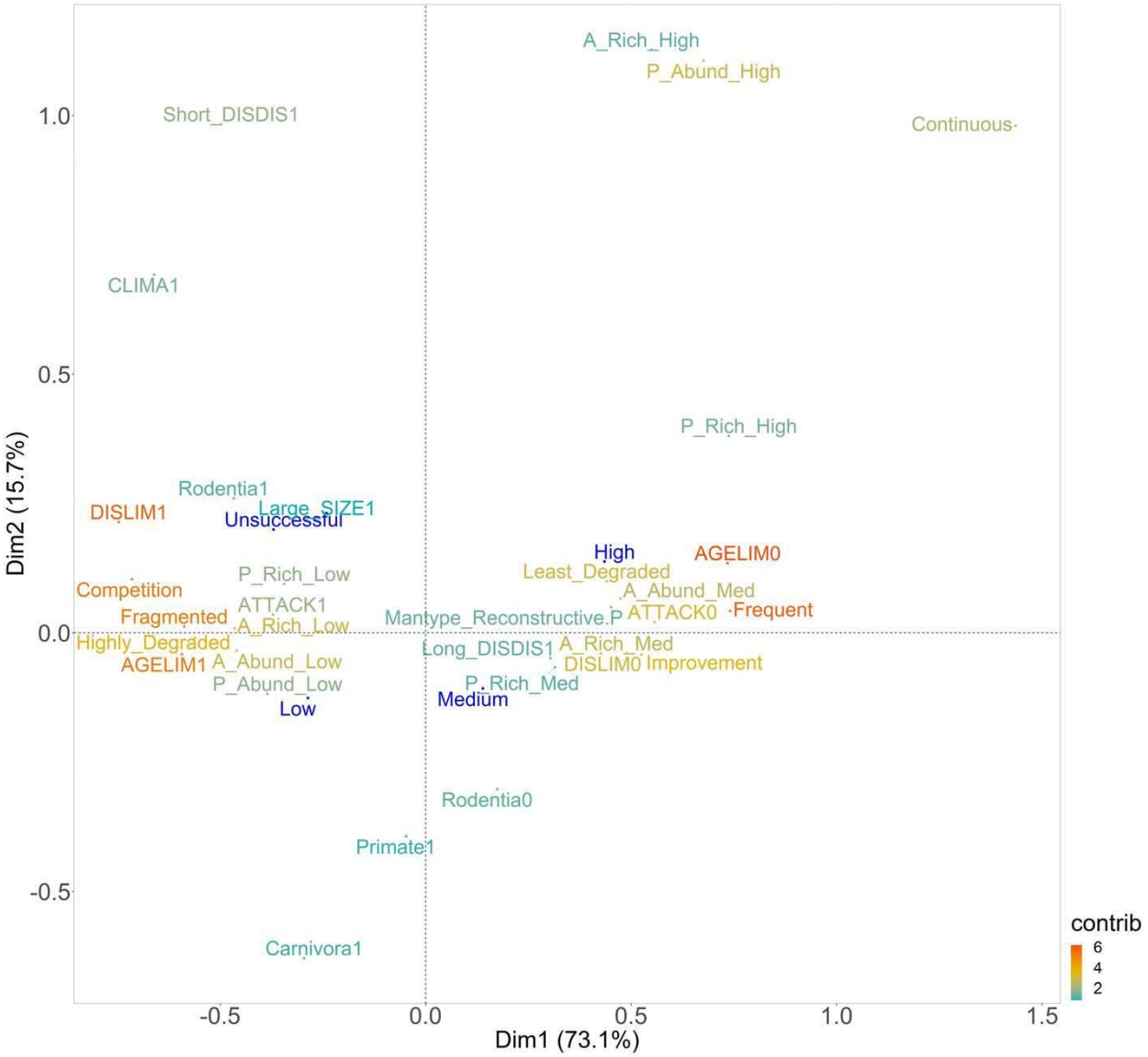


Figure 2.3. Variable contribution for "high", "medium", "low", and "unsuccessful" restoration success (blue labels) in tropical biomes, defined by two-way Correspondence Analysis. (See Appendix 1 Supplement S2 and Table S1 for variable codes and descriptions). Note that only the 32 variables with the highest contribution are shown.

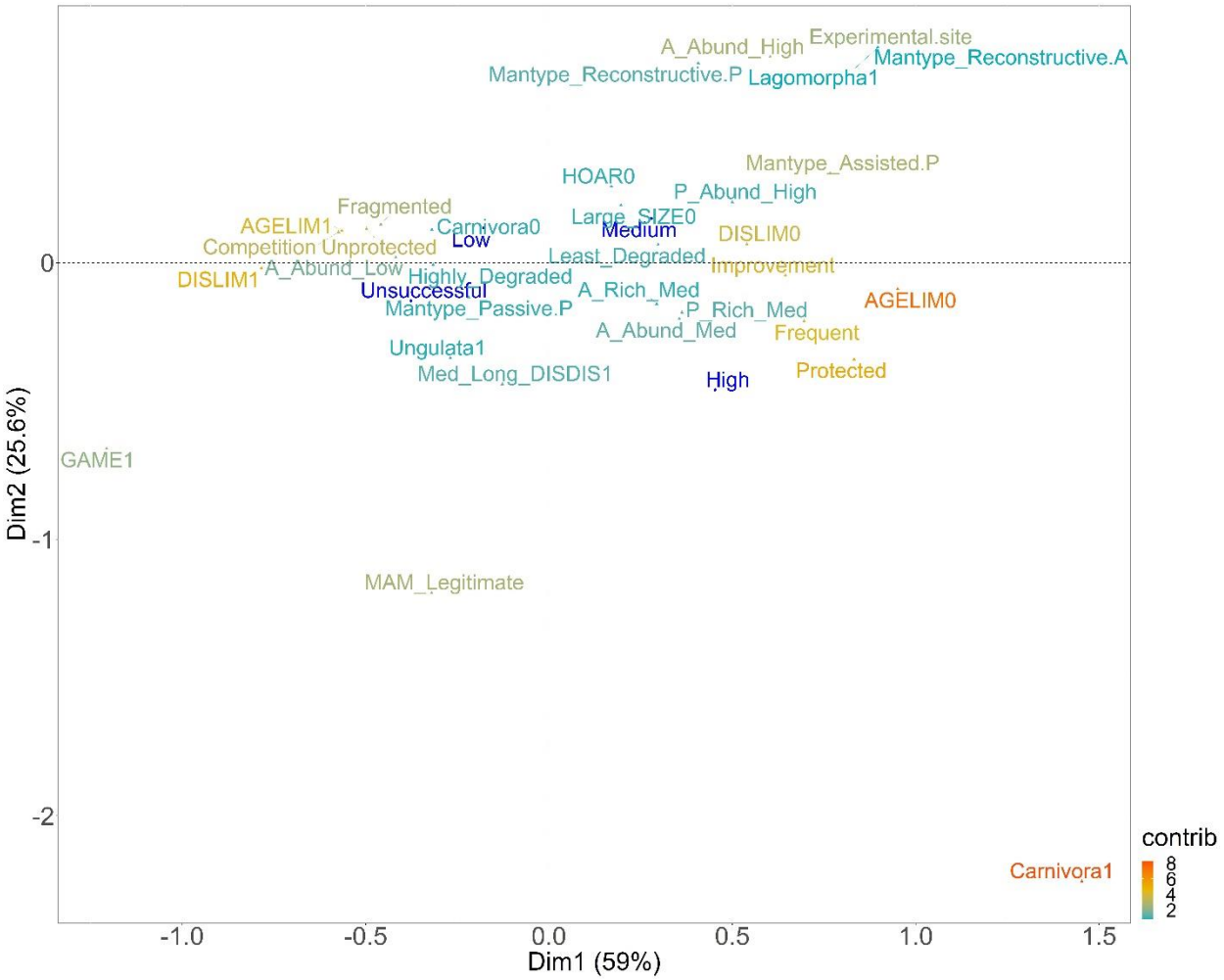


Figure 2.4. Variable contribution for "high", "medium", "low", and "unsuccessful" restoration success (blue labels) in temperate biomes, defined by two-way Correspondence Analysis. (See Appendix 1 Supplement S2 and Table S1 for variable codes and descriptions). Note that only the 32 variables with the highest contribution are shown.

For all biome types, the Classification Tree layout showed that the overall probability of restoration success was 81% (Appendix 1 Supplement S5A) and that the quality of representation of the CTA was 92%. Out of the extrinsic factors checked, the ones with major importance involving a positive restoration outcome, defined by the Gini Index, were close distance to reference habitat, "improvement" micro-environmental conditions, higher restoration age, not being subjected to seed attack, assisted plant restoration approach and "frequent" or "continuous" forest cover. Furthermore, the most important intrinsic dispersal factors involving effective restoration were

"medium" seed size, "high" or "medium" plant species richness and "medium" animal seed dispersers' abundance (Appendix 1 Supplement S5A).

For tropical systems, the overall probability of restoration success was 82% and the quality of representation was 93%, whereas for temperate systems, it was 79%, and 90%, respectively (Appendix 1 Supplement S5B, C). Extrinsic factors that showed major importance in the effective restoration outcome of tropical forests were higher restoration age, "improvement" of micro-environmental conditions, having a close reference habitat and an assisted or reconstructive restoration approach (Appendix 1 Supplement S5B), while only "frequent" or "continuous" forest cover was relevant for temperate biomes (Appendix 1 Supplement S5C). Regarding intrinsic factors, for tropical and temperate forests, "medium" and "long" animal seed-dispersal distance ability were the only intrinsic factors in common favoring restoration success. Across biomes, seed size, bird frugivory type, and "high" and "medium" plant species richness were important in tropical forests (Appendix 1 Supplement S5B) while lack of hoarder activity and "high" animal dispersers abundance were relevant in temperate ones (Appendix 1 Supplement S5C).

2.5. Discussion

To our knowledge, this review is the first to assess the contribution of different intrinsic and extrinsic factors affecting seed dispersal in forest restoration success globally, and separately in tropical and temperate biomes. Interestingly, most extrinsic factors had similar effects in restoration success worldwide (e.g., forest connectivity, time since restoration), while differences were observed for intrinsic dispersal factors in tropical and temperate forests. Specifically, those intrinsic dispersal factors related to dispersal syndromes and seed disperser traits were the most relevant in determining restoration in tropical and temperate forests. Yet, although our study was based on a thorough revision of the scientific literature (157 articles), we must acknowledge some limitations owing to the lack of studies comparing sites with and without animal-mediated dispersal.

We observed that the number of publications on this topic has gradually increased over time from 1996 until nowadays and specifically in tropical forests, whereas for temperate systems, this trend begun in 2002. This could be due to researchers taking higher action in forest restoration case

studies as commitments and initiatives to restore ecosystems and the services that they provide are becoming more widespread (Ockendon et al. 2018; Pereira & Navarro 2015; Romijn et al. 2019). Moreover, publications were significantly higher in tropical systems, where up to 90% of trees have traits adapted to animal-mediated seed dispersal (i.e., zoochory, Howe & Smallwood 1982; Howe 2016). Even so, there was a high variability in the number of publications among regions. For instance, publications were notably high in Brazil as it is one of the five countries encountering more than half of the world's forest, but also the country with the highest average annual net loss of forest area (FAO 2020). This scenario has made Brazil lead South America in public policies and legislation aimed at increasing the effectiveness of forest restoration (e.g., Atlantic Forest Restoration Pact) (Moreira da Silva et al. 2017). In contrast, other regions in Europe have also experienced forest loss but such rates have declined substantially following the land abandonment that began in the mid-twentieth century (FAO 2020; Palmero-Iniesta et al. 2020). Although forests are expanding in some regions, primary forests continue to disappear in Europe (FAO 2020; Sabatini et al. 2020) together with important ecosystem services that they provide (e.g., carbon storage, high levels of biodiversity, contribution to resilience) (Watson et al. 2018). Thus, ensuring protection and restoration of such forests has prompted restoration initiatives in Europe from a conservation perspective (Sabatini et al. 2020), and together with natural forest expansion has boosted restoration assessments in Europe in the past decade. Other territories in Southeastern Asia, Africa and Oceania, that have also experienced forest loss and a rapid decline in forest area (Betts et al. 2017), showed fewer number of publications. Future development of national and international networks of ecological restoration scientists and practitioners may promote such efforts in less considered regions.

Beside specific socio-economic attributes of each country and region, intrinsic and extrinsic dispersal factors have also shown to determine the result of the entire seed regeneration process (e.g., Crouzeilles et al. 2016; O'Donnel et al. 2018; Vallejo et al. 2012). In these lines, we found that the most used factors to assess the effects of seed dispersal in forest restoration success were the extrinsic ones. This could be due to the clear advantages of using extrinsic indicators that are easily measured, cost effective, and easily interpretable (Dey & Schweitzer 2014). For instance, frequently used factors such as information on restoration approaches, protection types and climatic conditions are easily accessible, provided by government agencies and other organizations involved in natural resource management. Regarding intrinsic factors, plant species richness and

abundance are relatively easy-to-measure indicators of plant species diversity (Lindenmayer et al. 2000) and were also widely used. Conversely, other intrinsic dispersal factors were not simple or inexpensive to measure, and usually required large investments of time. A good example is the richness and abundance of animal species, and the measurement of dispersed, germinated and established seeds (Aavik & Helm 2018; Iijima 2020).

Within intrinsic dispersal factors, our review showed that disperser and plant species richness and abundance highly contributed to successful restoration. Perhaps, such taxonomic richness reflects the diversity of dispersal traits among species (e.g., fruit handling methods and gut passage effects) and thus a broader spectrum of seeds to be dispersed in viable conditions for germination (Samuels & Levey 2005). Regarding animal seed dispersal distance ability, restoration resulted successful when animals dispersing seeds at long distances were involved, especially for tropical forests. This may be due to the presence of dispersers with higher movement capacity (e.g., birds), able to travel long distances and disperse seeds, affecting the spatial patterns of seed depositions and, ultimately, recruitment (González-Varo et al. 2019). Interestingly, relevant differences were found among tropical and temperate biomes regarding dispersal syndromes and frugivory types. For instance, we found that in temperate systems, carnivores highly contributed to seed dispersal, probably as they are known to act as legitimate seed disperser for many species (Gonzalez-Varo et al. 2013; Rubalcava-Castillo et al. 2021; Selwyn et al. 2020). Contrarily, large seed consumers (i.e., ungulates) were related to "low" and "unsuccessful" restoration as they usually grind ingested seeds (Selwyn et al. 2020). Also, considering that hunting mostly occurs where ungulates are present (Rooney et al. 2015), the negative effect of game on forest restoration might arise from the link between these two factors. Similarly to Galetti et al. (2015), we observed that although rodents may sometimes act as seed dispersers (Vander Wall et al. 2005), they were mostly associated with an unsuccessful restoration outcome in tropical forests. This could be due to population growth and activity increase of rodents owing to the reduced competition with larger seed disperser mammals, because of defaunation in altered landscapes or hunting pressure (Galetti et al. 2015; Wright et al. 2000). Also, rodents may differ in the way in which they interact with the plants, for instance, squirrels disperse a relatively high proportion of seeds, whereas mice disperse a smaller fraction as they tend to predate most seeds *in situ* (Gómez et al. 2019). Simultaneously, we also found that "large" sized seeds were more often associated with an "unsuccessful" restoration outcome in tropical forests. Again, this pattern could be related to defaunation and extreme hunting

pressure of the larger frugivorous mammals and birds responsible of the dispersal of large sized seeds (Wotton & Kelly 2012; Wright et al, 2000). Regarding temperate forests, "small" and "medium-sized" seeds were related to higher restoration success. This fact may suggest that in temperate biomes, seed dispersal is mostly driven by a more generalized avian seed dispersers' array which feeds on fruits with small seeds that are produced in large quantities and are consumed by a wide range of frugivorous birds (Herrera 1984; Howe 1986). These finding underline the importance of considering the variety of the plant-dispersal network models reflecting the outcome of restoration success and the particularities of different biomes to undertake the most suitable restoration approaches in different forest ecosystems.

Beyond the relevance of intrinsic dispersal factors, the analysis of the extrinsic factors related to socio-economic characteristics of each study site allowed us to detect that forest protection played a fundamental role in achieving restoration in forests worldwide, as it may be crucial for promoting the functioning in regenerating and managed forests (Sabatini et al. 2020). Regarding forest restoration approaches, differences were found between tropical and temperate forests: successful restoration occurred in temperate forests in which "assisted" restoration took place (e.g., non-native species removal, clear-cuts), while "reconstructive" restoration (e.g., reforestation) was the most successful option in tropical ones. For both biome types, these active restoration approaches suggest that these may have been highly disturbed areas, with a significant extent of deforestation, in combination with inadequate ecological conditions, resulting in slow or no recovery and thus, human intervention may have been required to actively accelerate forest regeneration (Holl 2017; Mittelman et al. 2020; Shoo 2016) and to recover stable, fully functional communities with reasonable investment requirements (Gann et al. 2019; SER 2021). As for the negative effects of passive restoration in temperate forests, there may exist several limiting factors (e.g., high seed predation, seedling herbivory, and stressful microclimatic conditions) which may limit and slow down passive restoration (Cruz-Alonso et al. 2019; Martínez-Muñoz et al. 2019; Rey-Benayas et al. 2015) and should be taken into consideration. Although these results suggest the advantage of active against passive restoration interventions, trade-offs between different interests and restoration objectives need to be examined to select the best restoration practices (e.g., Meli et al. 2017; Prach & del Moral 2015).

Furthermore, we found that studies covering forests with lower restoration time periods, independently of their biome type, tended to show "low" or "unsuccessful" restoration success suggesting that restoring conditions closer to those of reference forests face many challenges, not the least of which is the long timeframes involved (Sabatini et al. 2020). Longer restoration timeframes entail higher plant abundance, and thus, fruit resource, for which animal dispersers would be expected to spend more time in such areas, increasing their dispersal capacity (Crouzeilles et al. 2016) and comprising cascading effects on restoration success. Long term monitoring and evaluation of restoration actions will therefore provide higher quality to restoration assessments as the effects of restoration timeframes have shown to contribute to restoring forest complexity.

Additionally, other extrinsic factors related to the landscape scale contributed the most to restoration for all biome types. This is the case of forest cover and connectivity, which were the major factors limiting or favoring seed dispersal. Such factors are positively correlated with the disperser community abundance and composition (Bael et al. 2013; Falcão et al. 2018), and many authors suggest the benefits for seed rain and seedling recruitment (Chazdon et al. 2009; Tambosi et al. 2014). Accordingly, assuring connectivity between reference habitats and restoration sites would be essential as the lack of propagules could impede restoration of taxonomic and functional diversity (Hewitt & Kellman 2002; Ibáñez et al. 2014). In this line, as expected, our analysis also revealed that "highly degraded" sites often showed "unsuccessful" restoration for all biome types, as duration and severity of the disturbance reduce propagule availability and create competitive environmental conditions for regeneration (Martínez-Ramos et al. 2016). In addition, environmental effects at a more local scale were also found, as micro-environmental conditions of seed deposition sites showed major importance for the restoration outcome. This fact could mainly be due to stressful conditions such as high light and temperature levels and poor soils quality in disturbed sites, which limit seeding survival and growth, particularly of late successional species which are adapted to regenerate in the forest's understory (Holl 2012). Also, seed attacks, particularly in tropical biomes, seem to limit restoration success. This is not surprising as, for instance, post-dispersal predation by insects and seed-infecting fungi are some of the main drivers of seed mortality in tropical forests (Hulme 1998; Kulikowski et al. 2021; Sarmiento et al. 2017).

Our results suggest that to manage ecosystem restoration, plant animal interactions need to be addressed; specifically, accounting for the abundance of frugivorous animals as well as fruit resource availability should be considered as indicators of the quality of the dispersal function. Moreover, landscape features such as forest cover (connectivity) and habitat quality need to be considered to favour animal movements into restoration sites. Regarding differences among biomes, the results of our review would recommend that generalist seed dispersers (e.g., birds) should be promoted in temperate systems while large seed dispersers (e.g., primates) in tropical ones. Regarding the restoration approach to accomplish these recommendations, our results indicate that assisted restoration would suffice for temperate biome while more reconstructive efforts would be needed in tropical ecosystems.

2.6. Conclusions

Determining the efficacy and effects of seed dispersal on forest restoration is a complex task, but one that is essential both for evaluating returns on restoration investments, as well as for improving the quality of future efforts to repair degraded forests. As nations across the globe are working to develop forest restoration plans (e.g., Aichi Biodiversity Targets, E.U. Forest Strategy) it is important to use standardized methods for assessments of the restoration outcomes (e.g., Restoration Project Information Sharing Framework). Here, we highlight the importance of the part that animal mediated seed dispersal plays in forest ecosystem recovery, and how different intrinsic and extrinsic dispersal factors may contribute to such process globally, and specifically, for both tropical and temperate forests. While similar outcomes were observed regarding most extrinsic factors, some major differences were found within intrinsic dispersal factor across tropical and temperate biomes, suggesting the outermost importance of the variety of dispersal syndromes and traits in forest restoration. Thus, our findings provide valuable information on the most significant intrinsic and extrinsic dispersal factors influencing restoration success, while also informing on potential differences in the best restoration strategy to be applied in temperate and tropical biomes to achieve restoration goals. However, we acknowledge that distinguishing between levels of restoration success is a challenging task and future empirical research would be essential for understanding the full benefits of including animal mediated seed dispersal in forest restoration.

Chapter 3 -

Recent tree diversity increase in NE Iberian forests following intense management release: a task for animal-dispersed and drought tolerant species

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3.1. Abstract

Under increasing human-related threats to forests, many studies suggest that increasing tree species diversity may boost forest resilience by enhancing the range of species' responses to disturbances. However, it remains unclear whether passive or active forest management strategies should be applied to increase tree diversity. This issue would benefit from investigating which management and environmental factors, together with species' functional traits influence temporal changes in tree species diversity. We explored the influence of the bioclimatic region, land-use history, forest cover, protection, management, forest structure and changes in temperature and precipitation, to explain tree species diversity changes in NE Iberian forests, by comparing 3141 plots from the Spanish National Forest Inventory sampled between 1989 and 2016. Moreover, we assessed which species' functional traits (dispersal habit, drought and shade tolerance) were most relevant for diversity changes. After 27 years, tree species richness and diversity moderately increased in the tree and regeneration layers. This trend occurred mostly in long-established, non-recently managed forests and in those with a lower initial basal area. Increasing temperature had negative effects for diversity increase in the tree layer but positive for the regeneration compartment, while decreasing precipitation showed the opposite effects. Tree species with higher drought tolerance, and especially those animal-dispersed ones arriving from the regional pool, mostly contributed to the local diversity increase. This pattern occurred in all forest types, although the taxonomic array of species varied. The main drivers influencing the passive increase in tree species diversity suggest a primary role of diminishing forest exploitation in this recovery process, fine-tuned by climatic changes. This ecological scenario has particularly favored animal-dispersed tree species with higher drought tolerance, which mostly led the diversity increase. A higher presence of such highly mobile and drought tolerant species can be crucial to increase functional diversity and, ultimately, increase forest resilience under future scenarios of greater aridity. In light of these results, management strategies should continue fostering the restoration of diversity in once intensively exploited forests while ensuring the maintenance of the already gained tree species diversity.

Keywords: drought tolerance, forest diversity, functional diversity, land-use history, life history traits, passive restoration, seed dispersal.

3.2. Introduction

Natural disturbances are critical drivers of forest composition, structure, and functioning (Senf & Seidl, 2021). However, climate change, together with the release of past intensive human land use, may influence the ability of forests to recover after disturbances (Johnstone et al., 2016). Thus, identifying the underpinning mechanisms of forest resilience (i.e., the capacity of forests to absorb disturbances and re-organize after an environmental change, *sensu* Scheffer, 2020) has become a priority research topic to ensure the maintenance and provision of forest ecosystem functions and services (Johnstone et al., 2016).

Tree species diversity is considered one of the main attributes promoting forest resilience (Jactel et al., 2017; Messier et al., 2022) as it increases the range of tree responses to disturbances (i.e., the Insurance hypothesis by Yachi & Loreau, 1999) and provides functional complementarity fostering the efficient use of resources. Thus, numerous studies have emphasized the benefits of promoting tree species diversity by means of either passive natural regeneration or by active tree planting (Haberstroh & Werner, 2022; Messier et al., 2022). Yet, it has also been warned that increasing tree species diversity may require long time periods (Bauhus et al., 2017), and may be constrained by a myriad of factors influencing propagule availability and recruitment; such as changes in the climatic conditions (García-Valdés et al., 2015), land-use legacies (Cruz-Alonso et al., 2021), past and recent management (Chaudhary et al., 2016), forest protection (Lecina et al., 2019), and forest structure and cover (Crowther et al., 2015).

Due to the growing interest in the management and environmental factors shaping tree species diversity and the availability of databases resampling the same stands through long periods of time (e.g., National Forest Inventories), an increasing number of studies have examined the trends in tree species diversity through time at regional scales (Crockett et al., 2022; Sánchez de Dios et al., 2023; Vayreda et al., 2013; 2016). Interestingly, although they cover different biogeographic regions, all these studies point out towards an increase in tree species diversity during the last decades of the 20th Century onwards, reporting from moderate (Crocket et al. 2022) to rapid shifts (Vayreda et al., 2016), mainly driven by the effects of climate-warming and land-use changes. This increase in tree mixtures (i.e., the "renaissance" of mixed forests *sensu* Sánchez de Dios et al., 2023) may have important consequences for forest functioning such as increasing productivity (Bauhus et al., 2017) and resilience to disturbances (e.g., drought stress in Fichtner et al. 2020;

forest pests in Blanco-Rodríguez & Espelta, 2022). Nevertheless, the former studies have seldom explored whether such diversity increase arises from local forest dynamics (e.g., ingrowth of seedlings into the tree layer) or from the dispersal and recruitment of species from the regional pool.

In addition to assessing the factors triggering changes in tree species diversity, it will be essential to identify the functional traits of the species involved, as such traits will modulate their ability to surmount the ecological filters shaping recruitment success and, ultimately, the potential complementarity effects in mixed forests. Seed dispersal type has been identified as a primary trait influencing the filtering effects of dispersal, therefore which species, and in what abundance, can be found in an area (Selwyn et al., 2023). Yet, to understand the potential success in tree species recruitment after dispersal, other functional traits influencing environmental filtering such as shade and drought tolerance need to be considered (Thomson et al., 2010). Therefore, different plant functional traits need to be assembled to reveal how dispersal and establishment are linked.

The aims of this study were to analyze forest management and environmental factors influencing temporal changes in tree species richness and diversity in Catalan forests (NE Spain), to explore the role of species functional traits, and to assess whether diversity changes were driven by local dynamics at the plot level (i.e., ingrowth and regeneration) or by the arrival of new species from the regional pool. We investigated the role of the bioclimatic region, land-use legacies, forest cover, forest protection, past and recent management, forest structure, and changes in temperature and precipitation over the study period (1989-2016) and considered the changes in both the tree and the regeneration layers, to account for the patterns of tree diversity. Specifically, we addressed three main questions: (i) how have management practices and changes in climatic conditions influenced changes in tree species diversity over time?, (ii) were changes in tree species diversity mostly driven by local dynamics or by the arrival of species from nearby?, (iii) which functional traits (i.e., dispersal method, shade and drought tolerance) have contributed to changes in forest diversity? The results will help to calibrate the potential extent of passive changes in tree species diversity through time and develop management strategies to maintain and promote tree species diversity and, potentially, enhance forest resilience.

3.3. Materials and Methods

Study area

This research was conducted in Catalonia (NE of the Iberian Peninsula), bounded to the north by the Pyrenees and to the east by the Mediterranean Sea (Appendix 2 Fig. S1). Forests represent almost 40% of the territory and are characterized by a wide diversity of species and structures, reflecting an outstanding landscape heterogeneity and a long history of forest management (Roces-Díaz et al., 2021). Climate in the region is highly variable; affected by the latitudinal range, a rough topography, and the existence of an intense coastal-inland gradient, from warm Mediterranean to temperate-cold climatic regimes. Mean annual temperatures and rainfall range from 18°C and 400mm on the southern coast to 5°C and more than 1500 mm in mountain areas (Ninyerola et al., 2000). The most commonly occurring tree species at low altitudes are *Pinus halepensis*, *Quercus ilex and Q. faginea,* while *P. sylvestris*, *P. nigra*, *Q. pubescens* and *Fagus sylvatica* dominate at altitudes from 800 to 1500 m. Above 1500 m, forests are mostly dominated by *P. uncinata* and *Abies alba* (Roces-Díaz et al., 2021)

Experimental design

Forest inventory data

To investigate temporal changes in tree species richness and diversity we used data from the second (NFI2) and fourth (NFI4) Spanish National Forest Inventories which consist of permanent plots located in a 1 × 1 km grid covering all forested areas of Spain. Our study was based in Catalonia (Appendix 2 Fig. S1), where the NFI2 and NFI4 took place during 1989-1990 (hereafter 1989) and 2013-2016 (hereafter 2016), respectively (https://laboratoriforestal.creaf.cat/). After excluding burnt plots during the studied period (see Appendix 2 Fig. S1 for details), we obtained 3141 replicated plots systematically sampled in the NFI2 and NFI4 in Catalonia, from which we extracted the species composition and abundance of the tree (individuals ≥7.5 cm in dbh) and regeneration (individuals < 7.5 cm in dbh) layers. A total of 71 tree species were recorded in the assembly of the two forest inventories (Appendix 2 Table S1).

Species functional traits

As recruitment success in tree species is shaped both by their dispersal ability and their response to environmental filters (Cruz-Alonso et al., 2021), we performed a cluster classification according to seed dispersal type: animal-dispersed (dispersed by birds and mammals) *vs*. other dispersal methods, and to shade and drought tolerance. This classification was restricted to the most representative species for which data was available: we excluded tree species recorded in less than five plots (2‰ of the total number of plots) for both inventories, resulting in a total number of 43 species included for analysis (Appendix 2 Tables S1 and S2). Clustering resulted in four distinct groups of species, distinguishing: (C1) animal-dispersed species with lower drought and higher shade tolerance (e.g., *Fagus sylvatica*, *Prunus avium*, *Ilex aquifolium*), (C2) animal-dispersed with higher drought and lower shade tolerance (e.g., *Crataegus monogyna*, *Arbutus unedo*, *Quercus* spp.), (C3) species with other dispersal methods with lower drought and higher shade tolerance (e.g., *Abies alba*, *Fraxinus excelsior*, *Acer campestre*), and (C4) species with other dispersal methods and higher drought and lower shade tolerance (e.g., *P. nigra*, *P. halepensis*, *Acer monspesulanum*) (Appendix 2 Fig. S2). Notice that although a negative correlation could be expected between shade and drought tolerance, the Pearson correlation test showed a weak negative relationship ($r=-0.29$; $p<0.001$) and thus, we retained both characteristics for the cluster analysis.

Factors influencing temporal changes in tree species diversity

Bioclimatic region

We classified each plot according to the Bioclimatic Classification for Continental Spain, defined by the thermicity index (https://www.miteco.gob.es) in order to characterize the long-term climate for each study plot, and to identity potential vegetation types of each particular region. We considered three broad bioclimatic regions: (1) mesomediterranean, (2) supramediterranean, and (3) montane (Appendix 2 Fig. S1) which are characterized by coniferous, sclerophyllous and mixed forests in the mesomediterranean region; coniferous, semi-deciduous, sclerophyllous, and mixed forests in the supramediterranean region; and coniferous and mixed (coniferous-deciduous) forests in the monatane region (Roces-Díaz et al., 2021).

Land use history and forest cover

Land-use history was determined by overlapping the geographical location of each NFI plot with the orthoimages from the American flight B series conducted in Spain in 1956 (https://geoserveis.icgc.cat/icc_ortohistorica/wms/service). This allowed for the classification of the NFI plots into two types of land-use history trajectories: (1) "long existing forests" as those that were already present in 1956, and (2) "recent forests" as those that were located in pasturelands and croplands in 1956 and established after rural abandonment. The year 1956 is considered a suitable benchmark for distinguishing recent and long-existing forests in the region, because massive expansion of forests occurred during the second half of the 20th Century (Cervera et al., 2019). Moreover, previous studies suggest substantial differences in the structure, and functioning of both forest types (Basnou et al., 2016; Espelta et al., 2020). Additionally, the proportion of forest cover surrounding each NFI plot was calculated to account for forest connectivity in the landscape. For such, we used land cover maps derived from Landsat imagery corresponding to the years 1987 and 2017, which reasonably matched our study period (1989-2016) (González-Guerrero & Pons, 2020) and determined forest cover surrounding each NFI plot at 100m, 500m and 1000m. After calculating the Pearson correlation matrix for forest cover at the different distances and years (Appendix 2 Fig. S3), we selected the proportion of forest cover at 500m in 1987 as the most accurate measure of connectivity, similar to Basnou et al. 2016.

Forest protection

We identified those plots included in the Catalan system of protected areas (https://sig.gencat.cat/visors/enaturals.html). This network covers 31% of the territory and includes sites with strict, moderate and partial protection status (one national park, several natural parks, small partial national reserves, national interest sites, provincial parks and other Nature 2000 areas) (Lecina-Diaz et al., 2019). For simplicity, we categorized the plots as Non-Protected *vs*. Protected.

Past and recent forest management

The occurrence of past forest management (e.g., harvesting), prior to the NFI2, was obtained from evidence (e.g., stumps, woody debris) observed and recorded during the NFI2 field survey in 1989-1990. Additionally, we assessed the occurrence of recent forest management practices between

1986 and 2016 from the disturbance maps developed by Senf & Seidl (2021) using satellite data and manually interpreted reference plots.

Forest structure

The basal area (m^2 ha^{-1}) of the NFI2 plots was also used as a measure of the initial forest structure, as it may potentially influence forest dynamics and habitat suitability for tree establishment (Crowther et al., 2015).

Temperature and precipitation changes

We accounted for the effect of recent climate change (i.e., climate variation during the study period) by estimating the absolute change in temperature (ΔT [°C]) and the relative precipitation change (ΔP [%]) per plot, for the time between inventories. Following a similar approach to that of García-Valdés et al. (2021), we used aggregated data of the years 1988–1992 as representative of the NFI2 period, and the years 2011–2015 as to characterize the NFI4 period, obtained from the Climate Engine database (https://www.climateengine.org/) at 9.6 km daily resolution (AgERA5). The trends and summaries of temperature and precipitation changes for the study period are shown in Appendix 2 Fig. S4. Notice that changes in temperature and precipitation were not correlated (r=-0.01, p=0.03) and occurred in all bioclimatic regions.

Data analysis

Diversity changes between inventories

For each plot and inventory period, we calculated diversity metrics using Hill numbers of order q=0 (i.e., transformation of species richness, hereafter), q=1 (i.e., transformation the Shannon diversity index, hereafter) and q=2 (i.e., transformation of the Simpson diversity index, hereafter) (Chao et al., 2010). We also calculated the Pielou's Evenness Index to assess changes among species abundance distributions per plot (Wilsey & Potvin, 2000). For computing the diversity indexes, abundance was established considering the basal area for the tree layer and the count of individuals for the regeneration compartment (Cruz-Alonso et al. 2021). We calculated the absolute change for each diversity metric between NFI2 and NFI4 and conducted Wilcoxon-Man Whitney tests to determine significant changes. Additionally, we assessed the sensitivity of our results by repeating these analyses using a one-sample t-test on log ratios of change (i.e.,

Ln[DiversityNFI4/DiversityNFI2]). We then performed a permutational analysis of variance to test for systematic temporal turnover (i.e., overall directional shifts in composition) between both time periods for the abundance and the presence/absence of tree species composition, for the 3141 plots sampled (see Crockett et al., 2022 for a similar approach).

To analyze if the bioclimatic region, land-use history, forest cover, protection, past and recent management, forest structure and temperature and precipitation changes influenced changes in taxonomic diversity for the tree and the regeneration layers, we ran linear models for which the change of each diversity measure was the response variable. We fitted the models scaling continuous variables, without considering interactions given the large number of included explanatory effects, and we chose the best fit by using the Stepwise Algorithm (MASS *package*, Ciaburro, 2018) and selected the model with the lowest AIC using $\Delta AIC > 2$ as an indicator for supporting the more complex model. In addition, we computed the percentage of the variance explained by each variable using the Hierarchical Partitioning method (see Sánchez de Dios et al., 2023 for a similar approach).

Provenance likelihood and functional traits of newly recruited species

By comparing both NFIs we identified those plots that lost or gained species during the study period. For considering that a plot had lost a species, the species found in the NFI2 should be absent in both the tree and regeneration layers of the NFI4. Because the number of these plots was low (6.3% and 10.7% for the tree and regeneration layers, respectively) in comparison to the number of plots that gained species (39% and 30% for the tree and regeneration layers, respectively), we focused our analyses on those plots that gained species either by changing from monospecific to mixed or from mixed to more mixed stands. For such, we built a new metric based on the presence/absence information of each species in each plot and NFI period. This metric allowed us to address whether a new species which appeared in the tree or the regeneration layer in NFI4 inventory was already present in the NFI2 and thus recruited from inside the plot (therefore local pool; Fig. 3.1A,C); or the new recruited species was not present in the NFI2 plots and arrived from outside the plot (therefore regional pool; Fig. 3.1B,D).

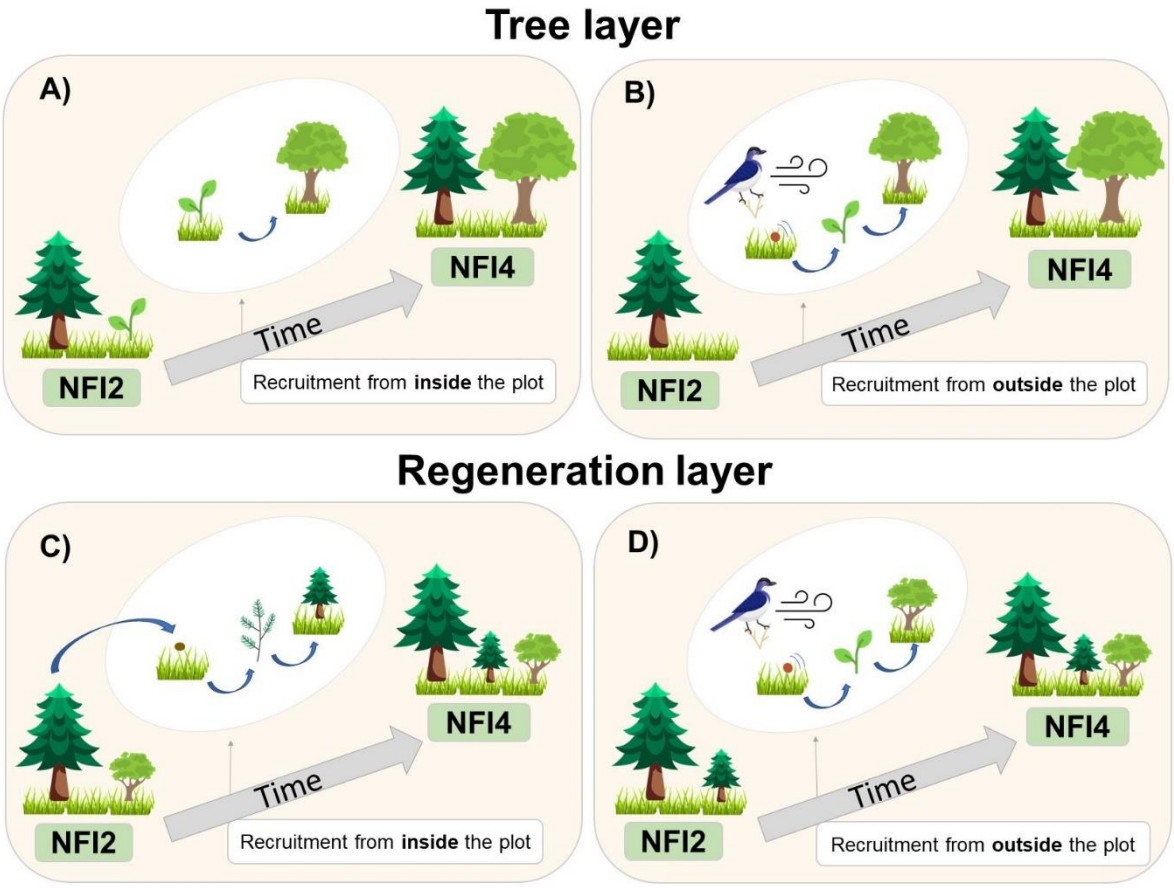


Figure 3.1. Representation of the origin (local vs. regional pool) of new species recruited in the plots surveyed in the forest inventory in 2016 (NFI4) for the tree (a, b) and regeneration layers (c, d), based on the presence/absence of such species in the previous inventory in 1989 (NFI2). We distinguished four alternative mechanisms for the recruitment of new species: (a) A new species recorded in the tree layer in the NFI4 was considered to be recruited from inside the plot (local pool) as a result of ingrowth if it was already present in the regeneration layer in the NFI2. (b) A new species recorded in the tree layer in the NFI4 was considered to be recruited from outside the plot (regional pool) when it was absent in the regeneration layer in the NFI2. (c) A new species recorded in the regeneration layer in the NFI4 was considered to be recruited from inside the plot (local pool) when it was absent in the regeneration layer but present in the tree layer in the NFI2. This process involved seed production by the local trees and the establishment of seedlings. (d) A new species recorded in the regeneration layer in the NFI4 was considered to be recruited from outside the plot (regional pool) when it was absent in the regeneration and tree layers in the NFI2.

For the subset of plots exhibiting an increase in species richness, we examined the role of functional traits on the chances of the different species to be recruited from inside or outside the plots. To do so, we carried out generalized linear models for the tree and the regeneration layers in which we analyzed the effects of the clustered functional traits and the management and environmental variables reported, on species provenance transformed into a binary variable (i.e., inside = 1, outside = 0) and fitted the best model using the same procedure as described above.

All models' residuals were checked for evidence of spatial autocorrelation and no sign of such was detected neither for the tree or the regeneration layers (Appendix 2 Fig. S5-S6).

3.4. Results

Temporal changes in tree species richness and diversity

The comparison between forest inventories showed a slight but significant increase in tree species richness, Shannon diversity index, and Simpson diversity index for both the tree and regeneration layers (Fig. 3.2), and these results were also confirmed by the sensitivity tests of log ratio changes (Appendix 2 Fig. S7). Conversely, we did not observe changes in the Pielou's evenness index for either the tree or regeneration layers (Fig. 3.2D,H). The increase in species richness and diversity was also supported by the permutation tests which showed significant compositional change for both the presence/absence and abundance of species for the tree and regeneration layers (Appendix 2 Table S3). As a result of the increase in tree species richness for the tree layer, 16% of the plots changed from monospecific to mixed stands, while 23% of mixed plots became more mixed during the studied period. For the regeneration layer, 21% of the monospecific plots gained species, while 9% of the mixed plots became more diverse. See Appendix 2 Fig. S8 for the spatial distribution of species richness changes for the tree and regeneration layers.

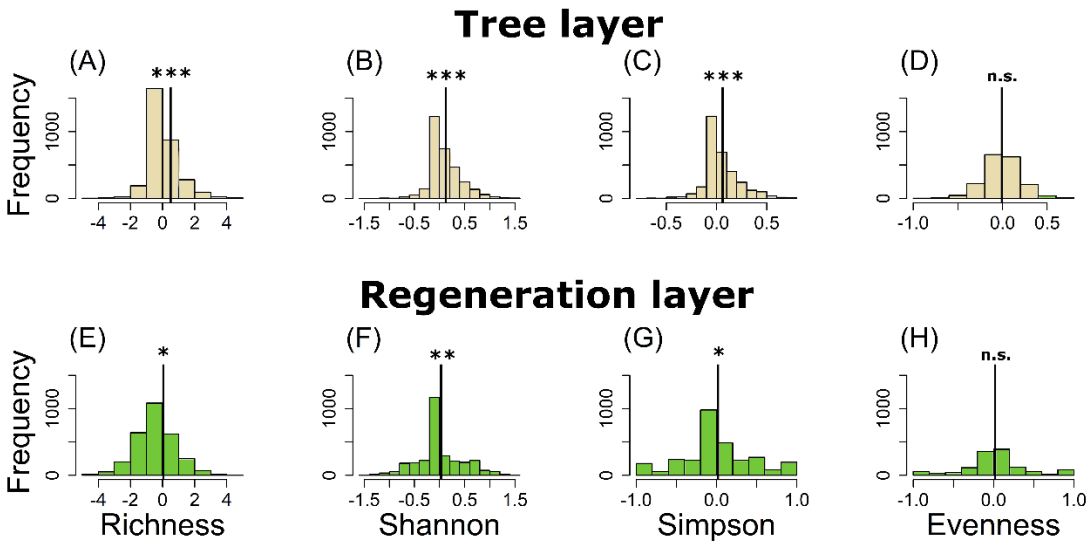


Figure 3.2. Mean change (black bar) from 1989 to 2016 for tree species richness, Shannon diversity index, Simpson diversity index and Pielou's evenness index for the tree (a–d) and the regeneration layers (e–h) for plots of the Spanish National Forest Inventory in Catalonia (NE Spain). Asterisks indicate significant differences according to the Wilcoxon–Mann–Whitney paired tests (* = 0.05; ** = 0.01; *** = 0.001; n.s. = non-significant). *N* = 3141 plots.

The main effects of the linear models explaining diversity change pointed out a significant increase in richness and diversity in the tree layer for the montane and supramediterranean regions compared to the mesomediterranean one, while for the regeneration layer the increase pattern was observed in all bioclimatic regions (Appendix 2 Tables S4-S9; Fig. 3.3). Also, changes in temperature and precipitation during the study period showed contrasting effects for the tree and regeneration layers: i.e., while for the tree layer, increasing temperature coupled with a lower decrease in precipitation negatively affected the increase in richness and diversity (Fig. 3.3A,B,C), it had positive effects for the regeneration layer (Fig. 3.3D,E,F). In addition to the influence of environmental effects, three variables related to forest management showed similar effects for the two compartments: i.e., the increase in species richness and diversity was higher in long-established forest plots while recent management and a higher total basal area showed a negative effect (Fig. 3.3). In addition, for the regeneration layer, past management did also negatively influence diversity (Fig. 3.3E) while forest protection showed a positive effect (Fig. 3.3D,E). For all models, the total percentage of the variance explained was less than 10% (Appendix 2 Tables

S4-S9), even so, the percentage of the variance explained by each variable's effect was significant in light of the results of the Hierarchical Partitioning analysis (Appendix 2 Fig. S9).

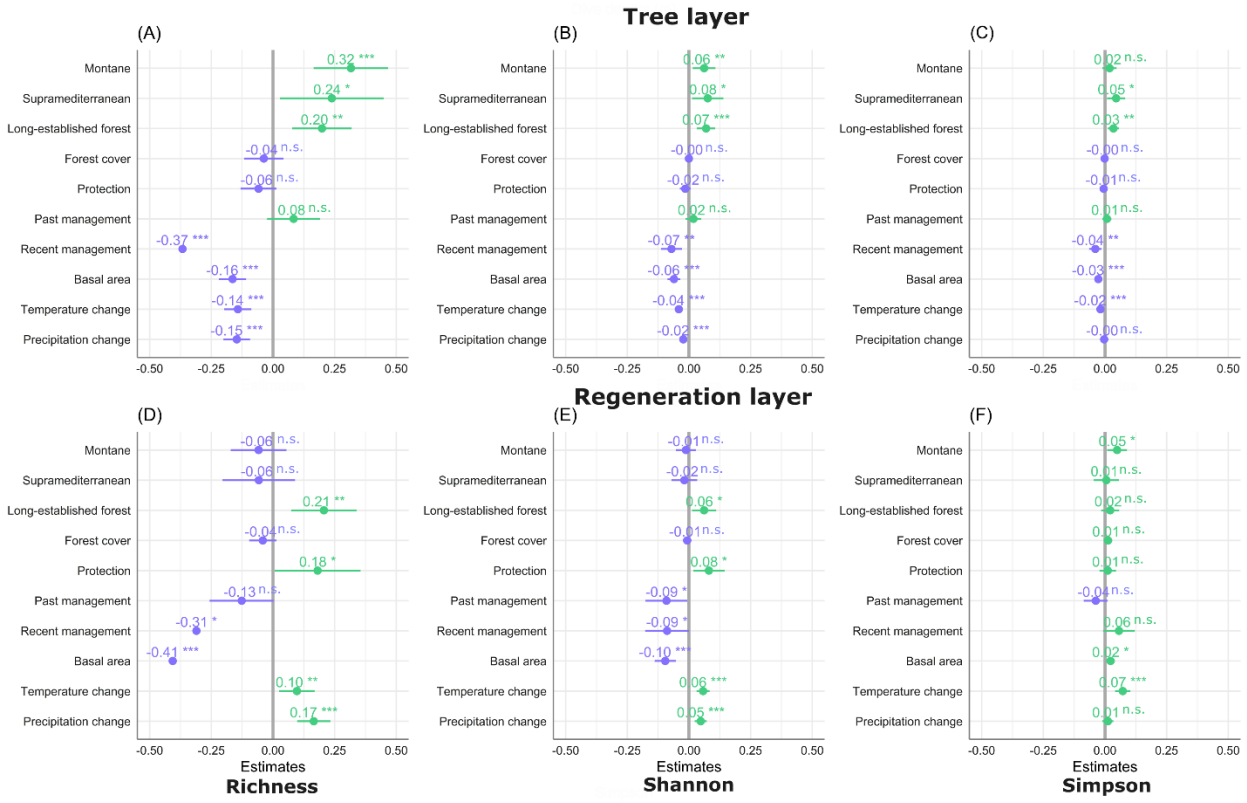


Figure 3.3. Parameter estimates for the linear models explaining the effects of forest management and environmental variables in the changes in tree species richness, Shannon diversity index and Simpson diversity index from 1989 to 2016 in the National Forest Inventory plots, for the tree (a–c) and the regeneration (d–f) layers. The explicative variables include the bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, and temperature and precipitation changes. Estimates, confidence intervals and *p*-values can be found in Appendix 2 Tables S4–S9. Asterisks indicate the significance of each effect (* = 0.05; ** = 0.01; *** = 0.001; n.s. = non-significant).

Provenance likelihood and functional traits of newly recruited species

As shown in Fig. 3.4, for the subset of plots that experienced an increase in tree species richness, most recruitment events of new species corresponded to species with higher drought tolerance both in the tree and the regeneration layers, (ca. 75% and 65% of events, respectively), primarily dispersed by animals (Cluster 2; ca. 60% and 50%, respectively) and secondarily by other methods (Cluster 4; ca. 20% for both the tree and regeneration layers).

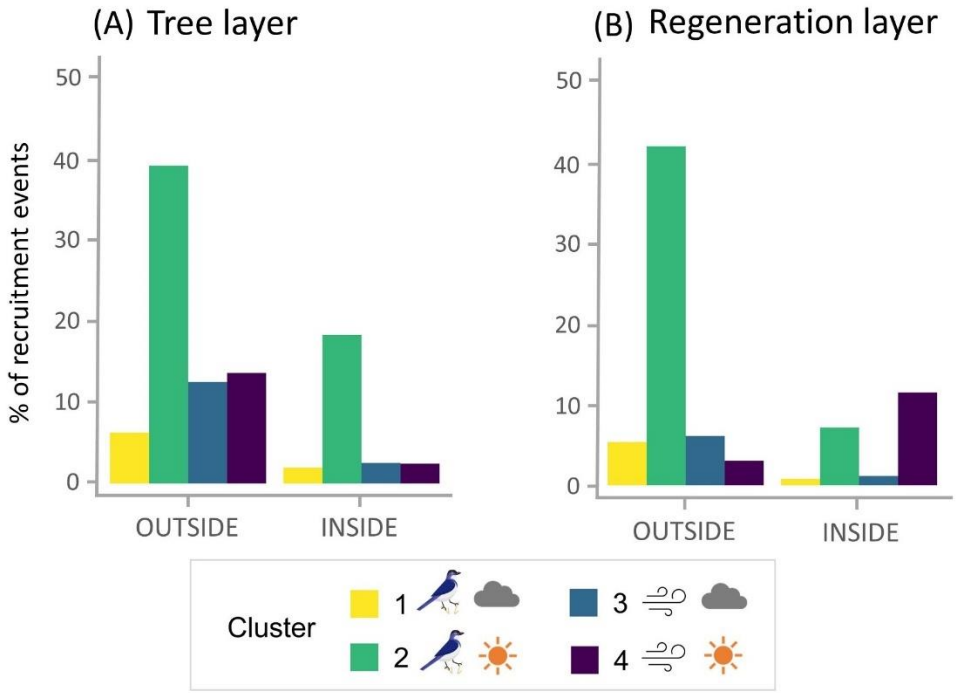


Figure 3.4. Recruitment events (%) of tree species from inside or outside the plots for the tree (a) and regeneration (b) layers for the subset of plots where tree species richness increased. Species were classified according to their dispersal mode (animal vs. other methods) and drought and shade tolerance (Appendix 2 Fig. S2). Clusters: 1 (yellow) = animal-dispersed species with lower drought and higher shade tolerance; 2 (green) = animal-dispersed species with higher drought and lower shade tolerance; 3 (blue) = species with other dispersal methods with lower drought and higher shade tolerance; and 4 (purple) = species with other dispersal methods and higher drought and lower shade tolerance. Note that the number of recruitment events differs for the tree and regeneration layers as a different number of plots gained species during the study period.

Recruitment of new species in any of the two layers occurred from inside and outside the plots but differences were observed for the tree and the regeneration layer depending on the functional traits and some of the forest and environmental characteristics (Appendix 2 Tables S10-S11). For the tree layer, recruitment of animal-dispersed species with higher drought (i.e., Cluster 2) significantly corresponded to individuals arriving from outside the plots (Fig. 3.5A). Regarding environmental and management characteristics, higher values of forest cover surrounding the plots prompted the arrival and recruitment of these new species from outside the plots (Appendix 2 Table S10). While we did not observe any significant effects of the bioclimatic region, protection, recent management, basal area or changes in temperature and precipitation. For the regeneration layer, the prevalence in the recruitment of new species arriving from outside the plot only occurred in the montane bioclimatic region (Appendix 2 Table S11). In this layer, the preferential recruitment of animal-dispersed species with higher drought tolerance (i.e., Cluster 2) from outside the plots was only marginally significant (Appendix 2 Table S11, Fig. 3.5B), while species with similar levels of drought tolerance but non animal dispersed (i.e., Cluster 4) were significantly recruited from inside the plots (Appendix 2 Table S11, Fig. 3.5B). Similarly to the observations for the tree layer no effects of differences in land use history, forest protection and structure and changes on temperature and precipitation were observed. The performance measurement of the generalized linear model for the tree layer was slightly lower than for the regeneration layer, but both showed good classification fit values (ROC-AUC > 0.60, Appendix 2 Tables S10-S11).

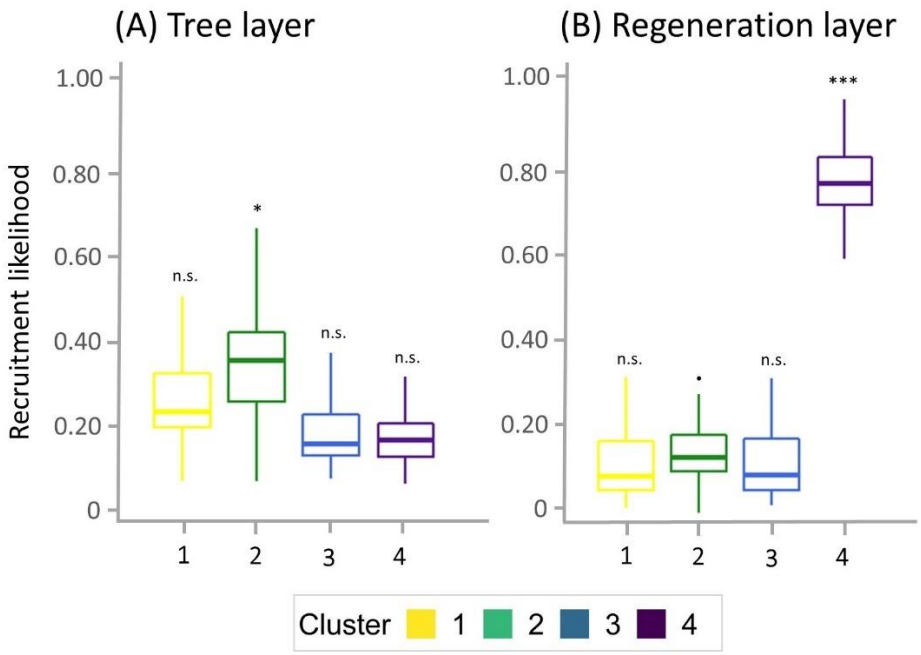


Figure 3.5. Recruitment likelihood probability from inside (i.e. 1) or outside (i.e. 0) the plots for species with different functional trait characteristics (i.e. cluster category) for the tree (a) and the regeneration (b) layers. Asterisks indicate the significance of differences in origin (i.e. inside vs. outside) of recruitment (· = 0.1; * = 0.05; *** = 0.001; n.s. = non-significant). See Fig. 4 for cluster codes.

3.5. Discussion

Increasing tree species diversity to adapt forests to climate change and human related disturbances, is a primary objective claimed by the scientific community (Messier et al., 2022) that is also gaining momentum in the political agendas (e.g., the European Union's Biodiversity Strategy for 2030). Yet, the time required to achieve this diversity increase, as well as which strategies (i.e., active or passive) should be applied are still under debate. Overall, the passive increase in tree species diversity reported here is in line with the signs of recovery of mixed forests reported in other studies varying in their spatial and temporal scale (Sánchez de Dios et al., 2023; Vayreda et al. 2013; 2016 for the Iberian Peninsula) but also in other biomes (e.g., Crockett et al. 2022 for northern forests), a pattern that has been attributed to both climate and forest management changes. In our region, the fact that the higher increase in tree species diversity occurred mostly in long-

established, non-recently managed forests and those that initially exhibited lower values of basal area (Appendix 2 Tables S4-S9; Fig. 3.3) reflects a trend towards the recovery of tree diversity, after a well-known history of extensive land-use changes and intense forest management that resulted in the impoverishment of tree diversity and the homogenization of forest composition (Cervera et al. 2019; Sánchez de Dios et al., 2023). Yet, our results highlight that after the release from intensive management, changes in tree diversity are also being fine-tuned by climatic (i.e., temperature and precipitation) trends (Roces Díaz et al. 2021; Cruz-Alonso et al. 2021). Notwithstanding this, we must acknowledge the low explanatory power of our models, in line with other studies that evaluated temporal changes in tree species diversity at local scales (α-diversity) (e.g., R^2<20% in Basnou et al., 2016; R^2<15% in Cruz-Alonso et al., 2021; R^2<5% in García-Valdés et al., 2021). This suggests the relevance that stochastic community processes (Crockett et al., 2022) or filters imposed by past disturbances events (Espelta et al., 2020) may have in shaping tree species diversity at small spatial scales, in comparison to more evident changes at the landscape level (Crockett et al., 2022; Cruz-Alonso et al., 2021; Espelta et al., 2020). In addition, the fact that the moderate diversity increase was mostly driven by changes in species richness, rather than by changes in evenness (i.e., no differences in the Pielou index, Fig. 3.2), suggests that the period analyzed (ca. 30 years) may still be too short to detect relevant effects of forest management and environmental changes in the dominance of particular tree species.

Non environmental factors influencing overall changes in tree species diversity showed similar effects for the tree and the regeneration layers: i.e., species richness and diversity increase was higher in long-existing forests than in recently established ones, and it was negatively affected by recent management and by higher values of basal area in the forest (Appendix 2 Tables S4-S9, Fig. 3.3). Considering that long and recently established forests in the area currently exhibit similar tree species richness and diversity (Basnou et al., 2016; Cruz-Alonso et al., 2021), the reported effect of land-use age on increasing forest diversity showcases a process of tree species recovery in long-existing forests where intensive past management and other disturbances had eroded their original tree diversity (Espelta et al., 2020). In addition to forest land-use age, our results revealed a self-evident negative effect of recent forest management for the increase in tree species diversity. These negative effects could be caused, for the tree layer, by the deliberate biased harvesting of particular tree species, as well as the negative effects of harvesting methods for the regeneration compartment (e.g., trampling, selective elimination of some particular tree species). Finally, the observed

negative influence of an initial high basal area for tree diversity increase (Appendix 2 Tables S4-S9, Fig. 3.3) could stem from two different effects. First, it may result that intense competition among trees in more developed stands determines scarce opportunities for the recruitment of new tree species (Vayreda et al., 2016). Second, we cannot discard that some forests with high basal area values correspond to mature forests where tree species richness has already reached, or approached, maximum levels (i.e., most, if not all, species present in the regional pool are already represented), and therefore further increases are unlikely to occur (Hilmers et al., 2018).

In addition to the paramount effects of factors related with land-use history and forest management, our study pinpointed a greater tree diversity increase for the tree layer in the supramediterranean and montane bioclimatic regions, which could be partially explained by the fact that the decrease in anthropogenic activities (i.e., forest exploitation, livestock grazing) occurred earlier and to a greater extent in mountain areas (Peñuelas et al., 2017). Moreover, differences in temperature and particularly in precipitation between the two inventories also affected the possibility of tree species diversity increase with contrasting importance and results for the tree and the regeneration layers: i.e., for the tree layer increase in diversity was lower in forests that experienced higher warming or a lower decrease in precipitation while the reverse situation was observed for the regeneration compartment (Appendix 2 Tables S4-S9, Fig. 3.3). The patterns observed for tree layer could be related with the observed higher occurrence and impact of tree decay and mortality episodes in areas that are becoming warmer but relatively stable in precipitation and are occupied by species at their southernmost distribution limit (e.g., *Pinus sylvestris, Fagus sylvatica*), more sensitive to increasing drought events than Mediterranean drought-adapted species (Chaparro et al., 2016,). In contrast, the positive effects observed for the same climatic trends for the regeneration layer could stem from the opportunities for seedling recruitment appearing in those forests that are experiencing tree decay and morality episodes (see for recruitment opportunities related to drought effects: Espelta et al., 2011). Nevertheless, temperature and precipitation changes had lower relevance in comparison to forest management effects (i.e., basal area) in driving changes in tree species diversity (Fig. 3.3; Appendix 2 Fig. S9). This pattern was also observed by other studies investigating temporal changes in the provision of ecosystem services in the same study area (Roces-Díaz et al., 2021) and highlight that climate change effects are not yet the main drivers of forests dynamics compared to the release in forest management.

The more relevant species contributing to the observed increase in tree diversity were those with higher drought and lower shade tolerance habit (i.e., Clusters 2 and 4 in Fig. 3.4) and, particularly by those animal-dispersed species (i.e., Cluster 2 in Fig. 3.4). The advantages of relatively high drought tolerance traits are consistent with the characteristics of the forests experiencing higher diversity increase: i.e., (open) forests with lower initial basal area (Fig. 3.3). In addition, the combination of these ecophysiological traits with animal seed dispersal may be especially appropriate to surmount the dispersal and environmental filters constraining tree recruitment in forest landscapes secularly affected by intense exploitation and habitat fragmentation in a climate characterized by water stress. In this scenario, seeds of animal-dispersed species can reach longer distances than those dispersed by other methods resulting often in an overrepresentation of the former species in highly isolated patches (Basnou et al., 2016). In addition, the directional dispersal of seeds towards suitable microsites (e.g., under shrubs) by the seed dispersers involved (e.g., *Garrulus glandarius*, *Pica pica*, *Turdus* spp., *Apodemus sylvaticus* in the region) and their catching behavior (e.g., protecting seeds under litterfall), may facilitate the successful establishment and growth, especially in a climate (i.e., Mediterranean-climate) with chronic water stress (Zavala et al., 2011; Martínez-Baroja et al., 2019). Interestingly, the genus *Quercus*, dominates the cluster of animal dispersed species with higher drought tolerance chiefly contributing to forest diversity (Appendix 2 Fig. S10A); a result that is in line with the recently reported expansion of oaks in Spanish forests (Sánchez de Dios et al., 2023; Vayreda et al., 2016). Yet, despite this relevance, it is important to highlight that other species and genus from the same cluster (e.g., *Sorbus* spp., *C. monogyna*, *Phillyrea latifolia*, *A. unedo* in Appendix 2 Fig. S10A) are also contributing to forest diversity increase. Thus, the key role of animal dispersed species with higher drought tolerance for tree diversity increase appears replicated in all bioclimatic regions, although involving different taxonomic identities: e.g., *A. unedo* in mesomediterranean pine forests while *C. monogyna* in montane ones (Appendix 2 Fig. S10A). In all cases, higher forest cover appears to be a relevant factor driving the likelihood of recruitment of these species from the regional pool (Appendix 2 Table S10), in line with the general benefits of connectivity among forest patches for seed dispersal by animals emphasized in previous studies (Selwyn et al., 2023).

Although the increase in species diversity was driven by the incorporation of new species either in the tree or the regeneration layer from both the local and regional pools (i.e., inside or outside the plots), our analyses revealed differences for the two compartments (Fig. 3.5). For the tree layer the preeminent contribution of animal dispersed species arriving from outside the plots is consistent with a massive early arrival of seeds of these species and their growth in monospecific conifer forests (Appendix 2 Fig. S11A, see also Gómez 2003). This process would reflect the classical Mediterranean forest succession path of pine-oak forests as a transitional stage leading to oak-dominated forests (Zavala et al., 2011). For the regeneration layer, the advanced contribution of species with higher drought and lower shade tolerance but non-animal dispersed (Appendix 2 Fig. S10B) mostly corresponded to conifers recruited in plots dominated by broadleaved species in the NFI2 (Appendix 2 Fig. S11B). Such contribution of conifers to increase the diversity of the regeneration layer could be related to recent extreme drought events and other forest decay episodes that severely affected broadleaved species (Chaparro et al., 2016). In contrast with the more classical successional theories, this situation would highlight that mixed conifer-broadleaved forests could increasingly become a stable alternative successional scenario under the current effects of climate change (Sánchez de Dios, 2023).

Ultimately, the higher recruitment of drought-tolerant species reported in our study could be crucial to enhance the resilience of NE Iberian forests under an aridity increase derived from climate change (Garcia-Valdés et al. 2021). On the one hand, this benefit would be achieved *per se* by the benefits of the particular functional traits of these newly recruited species to surmount water shortage. In addition, resilience in more diverse forests can also be promoted by the facilitative effects of higher levels of resource partitioning (e.g., soil water) among different neighbors (Grossiord et al. 2019, Pretzsch et al. 2013, Fichtner et al. 2020) or other effects such as microclimate partitioning or biotic facilitation. In this line, future research should be aimed to gain a more precise knowledge of the functional complementarity existing among the different species involved in the recent assembly of the mixed forests reported in this study.

3.6. Conclusions

For the last ca. 27 years, tree species richness and diversity has slightly increased in NE Iberian forests, influenced mostly by land use history, a release in the intensity of exploitation and changes in temperature and precipitation trends. Regarding forest characteristics, the fact that diversity increase was higher in long-existing forests highlights the need to foster the restoration of diversity in those secularly disturbed forests. In this line, shifting the exploitation towards more recently established and highly productive forests (Frei et al., 2023) could be considered to encourage this restoration process. In addition, the negative consequences of recent forest management for tree species diversity also stresses the need to promote silvicultural practices tailored towards biodiversity conservation (e.g., close to nature forestry). This scenario could benefit the establishment of animal dispersed tree species, which in combination with a higher drought tolerance are the ones leading the increase in tree species diversity. Ultimately, a higher presence of such highly mobile species may promote forests' "insurance capacity" (Messier et al., 2022) by enhancing their ability to resist droughts and, potentially, other human threats.

Chapter 4 -

Quantifying the impacts of rewilding on ecosystem resilience to disturbances: a global meta-analysis

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4.1. Abstract

Rewilding is one approach to restoration that aims at restoring natural self-sustaining ecosystems, allowing natural processes to resume by targeting an increase in trophic complexity, disturbance stochasticity, and dispersal, while minimizing human interventions. These components have also been argued to enhance ecosystem resilience, yet this claim has barely been specifically addressed. We conducted a meta-analysis to explore whether rewilding interventions aimed at increasing biodiversity (i.e., trophic complexity), disturbance stochasticity or connectivity increase ecosystem resilience to future abiotic and biotic disturbances. We integrated two recently developed operational frameworks to address rewilding and resilience and scrutinized the outcomes of 42 case studies (305 observations). We found that, overall, the three abovementioned rewilding components increased resilience of variables related to demography, biodiversity, biophysical characteristics and the disturbance regime characteristics. Yet, this result was influenced by the nature of the disturbance and the resilience approach, with lower success reported for abiotic disturbances (drought and fire) and socio-ecological resilience. While interventions targeting only disturbance stochasticity or biodiversity and disturbance stochasticity together showed positive effects, interventions targeting the trophic complexity alone contributed less to system variables related to biodiversity. The most common rewilding interventions, such as domestic and wild herbivore introductions and invasive plant removals, enhanced resilience towards biotic disturbances (i.e., invasions). We also found that some particular resilience contexts (socio-ecological systems) lack sufficient observations to allow clear conclusions. Overall, our results empirically demonstrate the predominantly positive effects of rewilding on ecosystem resilience, underpinning the potential of this approach for preparing for the uncertain effects of increasing climate change and associated disturbances yet acknowledging some limitations depending on the nature of the disturbance.

Keywords: biodiversity, climate change adaptation, dispersal, recovery, resistance, restoration, stochasticity, trophic complexity

4.2. Introduction

The world is grappling with an accelerating dual crisis of climate change and biodiversity loss, both of which are intricately connected and mutually reinforcing (O'Connor et al., 2020). The rapid rise in global temperatures and occurrence of disturbance events (e.g., flooding, heat waves, wildfires and drought episodes), coupled with habitat destruction and degradation, underscore the urgent need for initiatives aimed at restoring ecosystems and enhancing their resilience. Global and regional policies, such as the Convention on Biological Diversity (CBD, 2010), the UN Decade on Ecosystem Restoration (2021–2030) (UN, 2019), or the EU Green Deal (EC, 2019) and the Nature Restoration Law (2024), are examples of awareness and efforts to mitigate climate change impacts while simultaneously protecting and rehabilitating natural habitats facing uncertain ecological scenarios.

Rewilding, a concept initially developed in the circles of conservation biology (Soulé & Noss, 1998), has evolved and been progressively identified as a restoration strategy that emphasizes the recovery of self-sustaining complex ecosystems by allowing natural processes to resume trophic complexity, stochastic disturbances, and dispersal, while minimizing human intervention (Perino et al., 2019; Torres et al., 2018). Beyond its proven direct benefits for restoring and conserving biodiversity, natural disturbance regimes and landscape connectivity, rewilding is also expected to contribute significantly to enhance ecosystem resilience under the current scenario of climate change (Jarvie & Svenning, 2018; Perino et al., 2019; Svenning, 2020). For instance, strict fire suppression policies may strongly erode habitat conditions, deplete biodiversity and increase the risk of high-intensity wildfires (e.g., Brown et al., 2019; Stephens et al., 2024), thus opening the way to efforts for restoring more natural fire regimes. Similarly, positive effects of increasing biodiversity through trophic complexity on resilience have also been demonstrated in relation to other disturbance types such as biological invasions as predation or herbivory may help in controlling invasive species (Guyton et al., 2020; Mungi et al., 2023). In the face of escalating environmental challenges, rewilding initiatives may be crucial not only to restore degraded ecosystems, but also to reinstate their ecological stability and contribute to both biodiversity conservation and climate change goals (Carroll & Noss, 2021; Cromsigt et al., 2018; Svenning, 2020). Yet as restoration projects may have initial success but may fail to sustain their goals over time once disturbances occur (e.g., Ballari et al., 2019; Cava et al., 2018; Travers et al., 2021), it

is necessary to review and assess their contribution to resilience (i.e., a system's ability to absorb disturbances, recover, and reorganize in the face of environmental variability; Folke et al., 2004; Scheffer et al., 2015) in new ecological scenarios characterized by the uncertainty of increasing disturbances.

To date, there have been few efforts to assess the contribution of rewilding initiatives to ecosystem resilience, most likely due to the difficulties associated with the operationalization of the resilience concept across the vast range of domains in which it is used (i.e., different approaches, multiple dimensions and metrics, imprecise timescales; Donohue et al., 2016; Gunderson, 2000; Nikinmaa et al., 2020). Yet recent frameworks for quantitatively assessing resilience, such as the Operational Resilience Framework (ORF; Lloret et al. 2024), facilitate the matter by providing unified terminology and a sequence of steps to assess resilience.

The benefits of rewilding on ecosystem resilience have been repeatedly suggested (Carroll & Noss, 2021; Navarro & Pereira, 2015; Svenning, 2020), yet this statement is to date based on indirect assumptions or inferences and not on comprehensive empirical evidence. Such evidence does exist, but it is scattered across case studies from a broad array of terrestrial ecosystems, which are affected by different disturbance types. Meta-analytical approaches may be highly suited to gather and screen this evidence and to identify trends in demographic processes, biodiversity patterns, biophysical characteristics and control of disturbances which would reflect the eventual benefits of rewilding for ecosystem resilience to climate change.

Here we present a meta-analysis to examine if, and by which mechanisms, rewilding interventions may increase ecosystem resilience in terrestrial ecosystems under increasing climate change and its associated disturbances. To achieve this objective, we coupled and unified the theoretical framework for assessing rewilding proposed by Perino et al. (2019) and the operational resilience framework developed by Lloret et al. (2024). This coupling allowed us to analyze the role of the three rewilding components proposed by Perino et al. (2019) - trophic complexity, disturbance stochasticity and dispersal - as resilience predictors (i.e., manageable characteristics that increase resilience in the ORF framework) in response to disturbances of system variables related to demographic processes, biodiversity patterns, biophysical characteristics and control of disturbances. Our research aimed to: (i) analyze and describe the available scientific literature assessing empirical measures of resilience in rewilding projects, (ii) evaluate the suitability of

rewilding projects pursuing the increase of trophic complexity, stochastic disturbances and dispersal on enhancing ecosystem resilience, (iii) particularly explore the potential impact of rewilding interventions aimed at increasing trophic complexity for ecosystem resilience to different disturbance types (note that a large number of rewilding projects have been focused on this target). With our findings, we aim to provide evidence-based suggestions to help guide future rewilding efforts in a time of increasing disturbances.

4.3. Materials and Methods

Unifying frameworks to assess resilience in rewilding projects

To date, the rewilding concept has evolved towards the inclusion of a range of diverse process-oriented and dynamic approaches focused in restoring biodiversity and ecosystem functioning (Fernandez et al., 2017). Here, we consider rewilding as a restoration approach that aims to promote self-regulating complex ecosystems by restoring non-human ecological processes while reducing human control and pressures (Perino et al., 2019), and assume that ecosystem complexity and functioning are maintained by the interactions among three critical components of natural ecosystem dynamics, i.e.: trophic complexity, the occurrence of stochastic disturbances, and the maintenance of dispersal. As so, following Perino et al. (2019) we considered a rewilding intervention to target: (i) trophic complexity when the aim was to increase compositional or functional diversity (e.g., by introducing or removing particular animal or plant species) hereafter "biodiversity" a more general term to acknowledge also changes not related with the trophic level , (ii) stochastic disturbance when the purpose was to release ecosystems from the strict anthropogenic control of disturbances (e.g., transit from the emphasis on fire suppression to the restoration of more natural or semi-natural fire regimes) hereafter "disturbance stochasticity", and (iii) dispersal when the focus was to improve functional connectivity among habitats allowing for the dispersal of species (i.e., reducing landscape fragmentation), hereafter "connectivity" (Perino et al., 2019; Torres et al., 2018).

On the other hand, resilience is a common target in environmental management and decision-making, and it can generally be described as the capacity of a system to absorb disturbances and recover and reorganize in a timely and efficient manner, retaining essentially a similar structure,

identity, feedbacks, and functions (Folke et al., 2004). This definition embeds the three classical approaches to resilience, that can be described as: i) engineering resilience: ability of the system to recover to its previous undisturbed state (Pimm, 1984), ii) ecological resilience: maximum change that a system can absorb without shifting to an alternative state (Holling, 1973), and (iii) socio-ecological resilience: capacity of a socio-ecological system to reorganize, adapt and continue to provide ecosystem services after disturbance (Folke, 2006). Due to its multiple interpretations, efforts have recently emerged to build operational resilience frameworks for its quantitative assessment and application (e.g., Nikinmaa et al., 2020). Here, we focus specifically on the operational resilience framework (ORF) by Lloret et al. (2024) which recognizes and relates several elements, including: (i) the resilience approach (i.e., engineering, ecological, socio-ecological), (ii) the system variables addressed (i.e., resilience of what sensu Carpenter et al. (2001), (iii) the type of disturbances and stressors acting at given spatiotemporal scales (resilience to what sensu Carpenter et al. (2001)), (iv) a reference state to be compared with, and (v) the metrics used to compare the observed system variables between the disturbed system and the reference state. These five elements fit into a rationale aimed at identifying variables (termed resilience predictors) that are suitable to be managed for increasing the resilience of the system (see Lloret et al. (2024) for a more extensive description). Notice that when connecting the two abovementioned theoretical frameworks, the resilience predictors in Lloret et al. (2024) correspond to the interventions aimed to restore the three rewilding components defined by Perino et al. (2019) (Fig. 4.1).

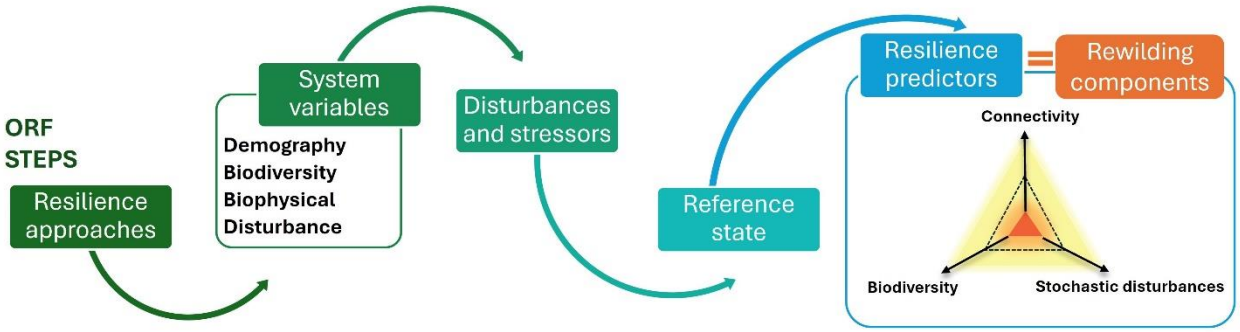


Figure 4.1. Representation of the coupling and unification of the two frameworks of Lloret et al. (2024) and Perino et al. (2019) used here to assess ecosystem resilience in rewilding projects. The Operational Resilience Framework (ORF) steps shown here correspond to a simplified version of the roadmap to assess resilience in Lloret et al. (2024). The final step links the resilience predictors (i.e., manageable variables suitable for increasing resilience) with the three rewilding components (biodiversity, stochastic disturbances, and connectivity) to be targeted in rewilding interventions to promote self-regulating complex ecosystems as defined by Perino et al. (2019).

Data acquisition and selection criteria

We followed the practical guide for conducting literature reviews in ecology and evolution developed by Foo et al. (2021), which provides recommendations on formulating questions for meta-analysis, and for obtaining representative samples of the research findings. To this end, we fitted the PICO statement defined by Richardson et al. (1995) based on identifying the following elements in the reviewed articles: (i) area that experienced either passive rewilding (e.g., spontaneous vegetation regeneration after land abandonment) or active rewilding interventions, and subsequently suffered a disturbance or stressor (Population in the PICO statement), (ii) rewilding intervention focusing on enhancing biodiversity, disturbance stochasticity, connectivity, or a combination of these resilience predictors (Intervention in the PICO statement), (iii) area that did not experience rewilding and experienced the same disturbance or stressor as the population (Comparator in the PICO statement), (iv) measure of the system variable in rewilded and non-rewilded areas after disturbance (Outcome in the PICO statement).

To address our research question, we searched published articles on 21/07/2023 and updated our search on 07/05/2024 using the Web of Science® database without restrictions on the publication year. Our search string for the title, abstract and keywords included terms related to "rewilding" or "restoration", "disturbance", and "resilience", and excluded those terms related to "aquatic systems". The term "restoration" was also included because rewilding is a relatively new concept, and the restoration literature could include projects that focused on increasing biodiversity, the recovery of stochastic disturbances or connectivity, without using the term "rewilding" (Mutillod et al., 2024). The search yielded a total of 879 papers. After in-depth screening, we discarded all articles that did not meet our PICO statement, as for instance they did not compare to a non-rewilded area or because resilience was mentioned but not measured. Finally, we retained 42 articles for data extraction (detailed ROSES diagram (Haddaway et al., 2018) in Appendix 3 Supplement S1).

Data extraction

We extracted variables that corresponded to the general characteristics of the study (e.g., coordinates, ecosystem type, time since treatment), the rewilding process (e.g., type of intervention, rewilding component according to Perino et al. 2019), the disturbance (e.g., disturbance agent, disturbance type), and the resilience (e.g., resilience approach, system variables) (Appendix 3 Supplement S2 reports the complete list of variables and descriptions). To quantify the contribution to resilience after the occurrence of a disturbance event, we noted and compared the means, variances, and sample sizes of the system variables for the rewilding treatment and the control (no-rewilding) considering the values before the disturbance event or a desired equivalent state (i.e., the reference state sensu Lloret et al, 2024). If measures were taken multiple times (e.g., a four-year experiment that was measured once per year), we considered only the last measure of the response variable because rewilding effects of the latest date would be more stable than those in the initial period. Whenever the data was not available in the main text or supplementary material but shown in figures, we used ImageJ (https://imagej.net/ij/index.html) to extract the data.

Rewilding interventions were categorized according to whether they targeted any of the three rewilding components, namely (i) biodiversity, (ii) stochastic disturbance, and (iii) connectivity (Table 4.1). When a case study targeted more than one rewilding component, they were all considered. The 45 system variables recorded (Table 4.2) were categorized into four broad types:

(i) individual characteristics and demographic processes (hereafter Demography), (ii) compositional, trophic, and functional biodiversity (hereafter Biodiversity), (iii) biophysical characteristics and structure (hereafter Biophysical) and (iv) characteristics of the disturbance regime (hereafter Disturbance). Some system variables were transformed to match with the resilience rationale of this study (e.g., mortality rates were converted into survival rates, or basal area or vegetation height in wildfire-related contexts were re-labelled as fuel load; see Table 4.2 for further details). For disturbances, mean values were multiplied by -1 to accurately reflect a reduction on the occurrence of disturbance (Monteagudo et al., 2023).

Table 4.1. Classification of rewilding interventions extracted from the primary studies according to the three rewilding components considered here. Note that we did not find any study which targeted the connectivity component alone, and that because of lack of representativeness the three studies targeting the biodiversity/connectivity component were included in the biodiversity component.

Rewilding intervention	**Rewilding component**	**(Number of observations, Number of primary studies)**
Animal introduction, animal removal, herbivory exclosure, invasive or non-native plant removal, plant introduction, animal protection, plant protection	Biodiversity	(163, 26)
Prescribed fire, herbivory, rooting	Disturbance stochasticity	(49, 5)
Any of the above trophic and disturbance interventions combined	Biodiversity/disturbance	(61, 8)
Animal introduction, animal removal	Biodiversity/connectivity	(22, 3)

Table 4.2. Classification of the system variables (response variables) extracted from the primary studies into four main categories. The most frequent measurement units and the number of observations and primary studies for each category are shown.

System variable category	System variable	Metric	(Number of observations, Number of primary studies)
Individual characteristics and demographic processes (Demography)	Animal abundance, animal density, animal visits, density of dead trees, dispersed seeds, drought tolerance, fruit removal, number of flowers, number of seeds, plant abundance, plant density, seedling recruitment, survival, tree growth, tree recruitment	Individuals·ha^{-1}, count, %, cm^2·year^{-1}, kg·ha^{-1}, µmol-1·FW, cm.	(114,36)
Compositional, trophic, and functional biodiversity (Biodiversity)	Plant diversity, animal diversity, plant-animal interactions, species turnover, functional redundancy	Richness, Shannon index, evenness, %.	(34,15)
Biophysical characteristics and structure (Biophysical)	Basal area, canopy height, carbon storage, vegetation cover, litter cover, area lost, bare soil, microbial biomass, NDVI, plant biomass, soil features, water content	m^2·ha^{-1}, m, %, kg·ha^{-1}, µmol CO_2·m^{-1}·s^{-1}, mg C·g^{-1}, g·g^{-1}.	(81,32)
Disturbance characteristics (Disturbance)	Browsing, fire likelihood, fuel load, invasive plant features (biomass, abundance, basal area, growth, cover, diversity, number of flowers, number of fruits, density, seedling recruitment, survival)	cm, cm^2, count, %, individuals·ha^{-1}, kg·ha^{-1}, m^2·ha^{-1}, m, richness, g/m^2.	76,40

Data analysis

Qualitative analysis (vote counting)

We first compiled, described and catalogued the available studies (James et al., 2016) on rewilding approaches and their impacts on ecosystem resilience to disturbances. Secondly, we performed a vote-counting analysis based on the direction effect, following the procedure of Light & Smith (2012). Interventions that significantly influenced resilience, either positively or negatively, were identified based on statistically significant effects ($P < 0.05$) reported in the primary studies. If the effect was not statistically significant, it was considered neutral, similarly to Monteagudo et al. (2023). Following these criteria, all 305 observations from the 42 primary studies were used for vote-counting of the effects of rewilding components and system variable categories, while 195 observations from 32 primary studies were used to analyze the effect of specific trophic rewilding interventions on resilience. Finally, we performed chi-squared tests to analyze whether the frequency of observed positive, neutral, and negative effects was statistically different from the expected frequency at random.

Quantitative analysis (meta-analysis)

To quantify the direction and magnitude of rewilding components on ecosystem resilience, we calculated the effect size for 280 observations from 37 primary articles. This was done by computing Hedges' g applying the escalc function (package "metafor"; Viechtbauer, 2010) using the measures of the system variables along with their variance and sample sizes for rewilded and non-rewilded areas. Mixed models adjusted for meta-analysis were fitted to analyze: (i) the overall effect of rewilding components, with and without considering different so called "moderators" in meta-analytical studies (i.e., system variable category, resilience approach, resilience dimension, disturbance agent, disturbance type, and ecosystem type), (ii) the individual effect of each rewilding component (i.e., biodiversity, disturbance stochasticity, biodiversity/disturbance) and its effect on each system variable category, and (iii) within the most frequently addressed rewilding component (i.e., biodiversity, see Results), the individual effect of the most representative interventions, namely, animal introductions, animal removals, plant introductions, and plant removals.

As most of the primary studies rendered several observations, models were fitted using random effect models for meta-analyses (rma.mv function of the R "metafor" package; Viechtbauer, 2010) with the identity of the primary study as a random effect to account for the lack of independence. Akaike's information criterion corrected for small sample sizes (AICc) was used to evaluate the effect of moderators based on backward elimination (Appendix 3 Supplement S3). Heterogeneity in effect size among moderator levels was estimated using the Q_M statistic. I^2 statistic was used to describe the percentage variation among primary studies that was due to heterogeneity rather than randomness. Finally, Rosenthal's fail-safe number was calculated to identify the number of primary studies needed to change the overall effect of the meta-analysis using the R "fsn" package (Fragkos et al., 2014).

4.4. Results

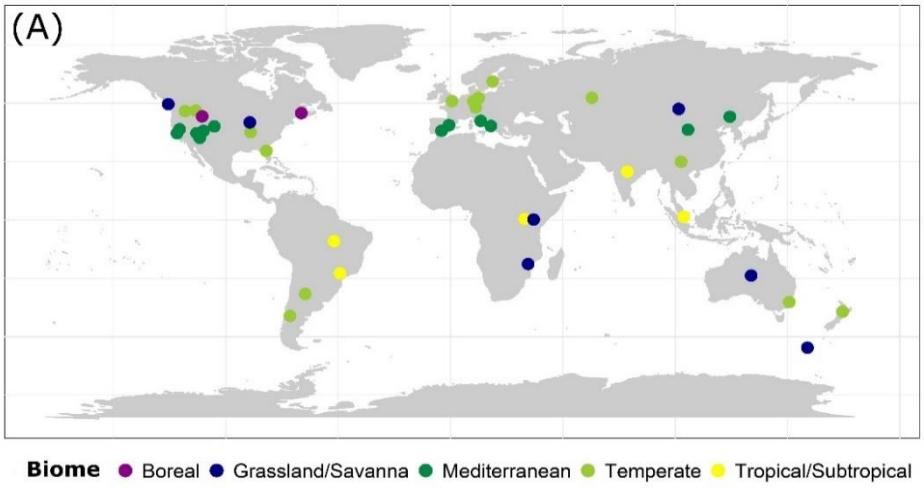
Dataset description

The 42 primary studies were published between 1998 and 2024 and were conducted in 19 countries distributed across five continents and five climatic zones according to the Köppen-Geiger climate classification (Fig. 4.2A). Most studies were in temperate forests (35%), followed by mediterranean woodlands (29%), temperate and subtropical grasslands/savannas (17%), tropical/subtropical forests (12%), and boreal/montane forests (7%). Regarding ecosystem type, most studies covered forests (57%) and grasslands (43%).

The primary causes of land degradation leading to the rewilding interventions conducted were highly variable and included fire exclusion (22%), livestock overgrazing (19%), agricultural practices (19%), defaunation (14%), plant invasions (12%), forest harvesting (7%), fire (5%), and mining (2%). 93% of the studies reported active rewilding interventions while 7% reported passive rewilding. As for the elements identified in the ORF, most studies (58%) addressed a complete resilience dimension (i.e., including both resistance and recovery) followed by resistance (28%) and recovery (14%). Rewilding interventions considered as resilience predictors in the ORF mostly targeted the biodiversity rewilding component (69%) followed by the biodiversity/disturbance (19%) and disturbance stochasticity alone (12%) (Fig. 4.2B). No primary studies were found for the dispersal component alone. Only three studies were obtained for the biodiversity/connectivity

component, which were included in the biodiversity component due to the low explanatory power for statistical analysis. The rewilding interventions reported mostly consisted of invasive or non-native plant removal (36%), wild herbivore introductions (22%) and prescribed fire (20%), followed by native plant introductions (11%), wild or domestic herbivore removals (7%), and plant replacement (i.e., remove non-native and introduction of native species, 4%).

The most frequent system variables corresponded to the categories of demography (37%), biophysical characteristics (27%), and disturbance characteristics (25%), while biodiversity (11%) was less common (Fig. 4.2B). Regarding disturbance agents, 41% were abiotic and 59% biotic, with the most frequent being fire and drought for the first group, and invasive species for the second group (Fig. 4.2B).



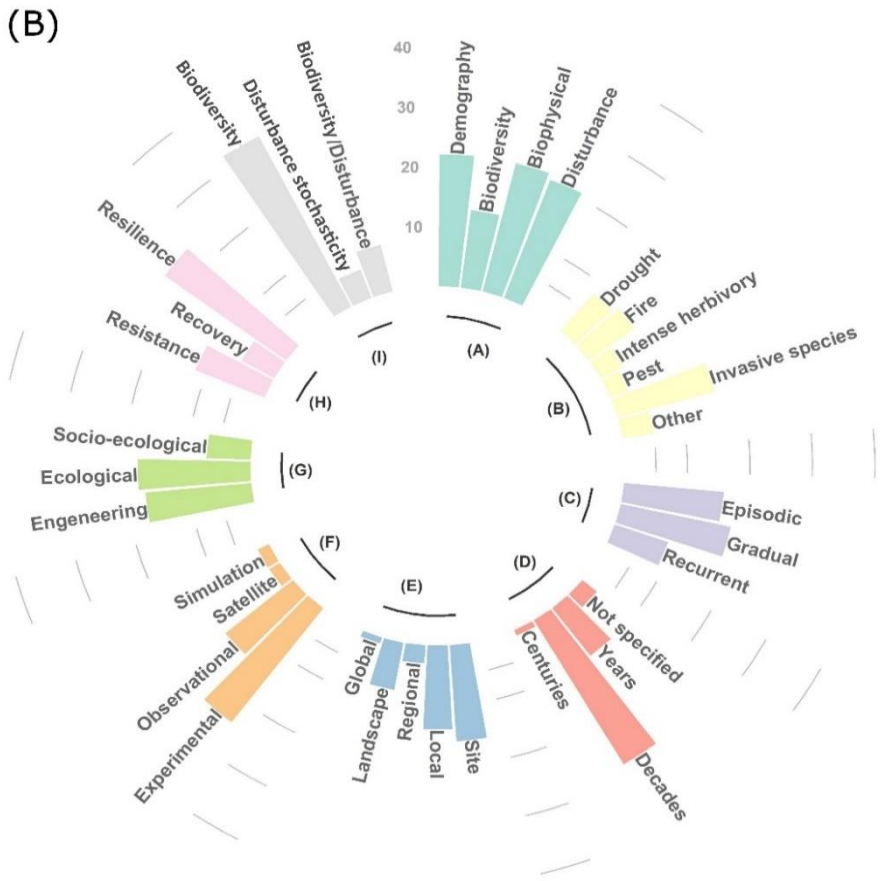


Figure 4.2. (A) Geographic distribution of the 42 primary studies selected. Each point indicates a study location, and colors illustrate biomes using the global Köppen-Geiger climate classification. (B) Distribution of the Operational Resilience Framework (ORF) elements: A: system variable categories; B: specific disturbance; C: disturbance type; D: temporal scale; E: spatial scale; F:

study type; G: resilience approach; H: resilience dimension; I: resilience predictors (i.e., rewilding components). For each ORF element, the number of studies with a particular category is shown. See Appendix 3 Supplement S2 for the complete list of variable descriptions.

Directional effects of rewilding on resilience (vote counting)

Overall, 68.2% of the observations included in the vote counting analysis reported a positive effect of rewilding on resilience after disturbances, 11.8% reported a neutral effect, and 20.0% reported a negative effect. The positive effect of rewilding was statistically significant for the three rewilding components together, as well as individually for each of them: i.e., biodiversity, disturbance stochasticity, and biodiversity/disturbance components (Fig. 4.3A, Appendix 3 Supplement S4). The benefits of rewilding to cope with disturbances were observed for all four categories of system variables: demography, biodiversity, biophysical characteristics, and disturbance characteristics (Fig. 4.3B; Appendix 3 Supplement S4). And when specifically focusing on the four types of interventions included in the biodiversity component of rewilding, we found significant positive effects for animal introduction, animal removal, plant introduction, and plant removal (Fig. 4.3C; Appendix 3 Supplement S4).

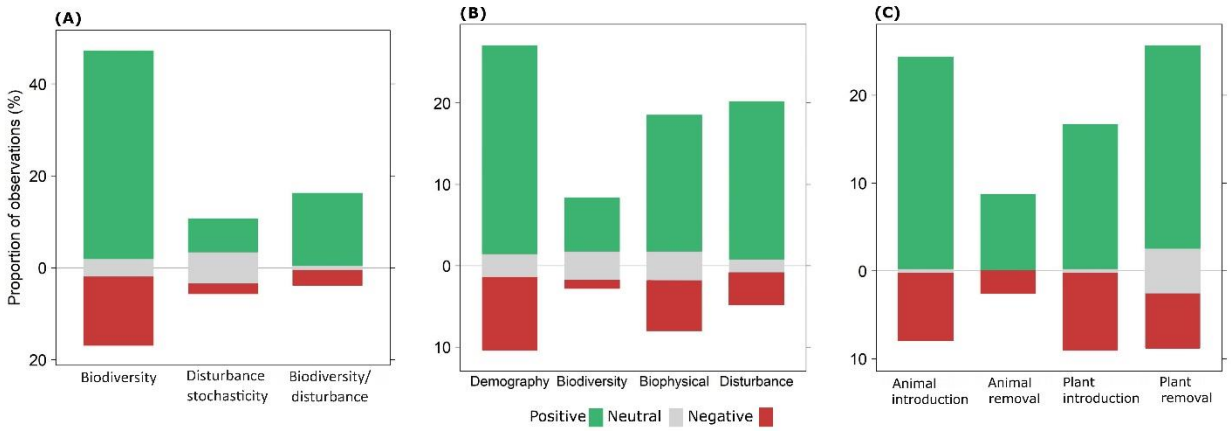


Figure 4.3. Proportion of observations showing the direction effect (positive, neutral or negative) of (A) rewilding components for ecosystem resilience ($n_{observations}$ = 305, $n_{primary\ studies}$ = 42), (B) system variable categories for which resilience was assessed ($n_{observations}$ = 305, $n_{primary\ studies}$ = 42),

and (C) specific rewilding interventions aimed at increasing biodiversity ($n_{observations}$ = 190, $n_{primary\ studies}$ = 26). N is the number of primary studies considered. Note that the proportion of observations represented in the figure are not cumulative.

Effect size and effect of moderators (meta-analysis)

The overall effect of all three rewilding components on resilience was positive and significant (Fig. 4.4; Appendix 3 Supplement S5) but showed high heterogeneity among observations (Q_{Total} = 8813.62, df = 279, P < 0.001). This later result suggests that heterogeneity was not explained by sampling error and justifies the inclusion of moderators in the model. Moreover, Rosenthal's fail-safe number showed that a very high number of observations (fsn = 202,975) would be needed to significantly change the direction of the effect size, underpinning the robustness of the meta-analysis conducted.

Rewilding had a positive and significant effect on resilience for the four system variable categories (Fig. 4.4; Appendix 3 Supplement S5). Regarding resilience approach and dimension, rewilding was positive and significant for engineering and ecological resilience but showed non-significant effects for socio-ecological resilience (Fig. 4.4; Appendix 3 Supplement S5). Rewilding had a positive and significant effect when addressing resistance and recovery together (i.e., complete resilience dimension) while showing non-significant effects when considering the two components alone and separated (Fig. 4.4; Appendix 3 Supplement S5). As for the disturbance agent, rewilding had a significant positive effect for ecosystem resilience to biotic disturbances while showing a negative effect for abiotic ones (Fig. 4.4; Appendix 3 Supplement S5). Regarding disturbance type, rewilding had a significant positive effect for gradual and recurrent disturbances, while there were no significant effects for episodic ones (Fig. 4.4; Appendix 3 Supplement S5). Finally, rewilding had significant positive effects on the resilience of both forests and grasslands (Fig. 4.4; Appendix 3 Supplement S5).

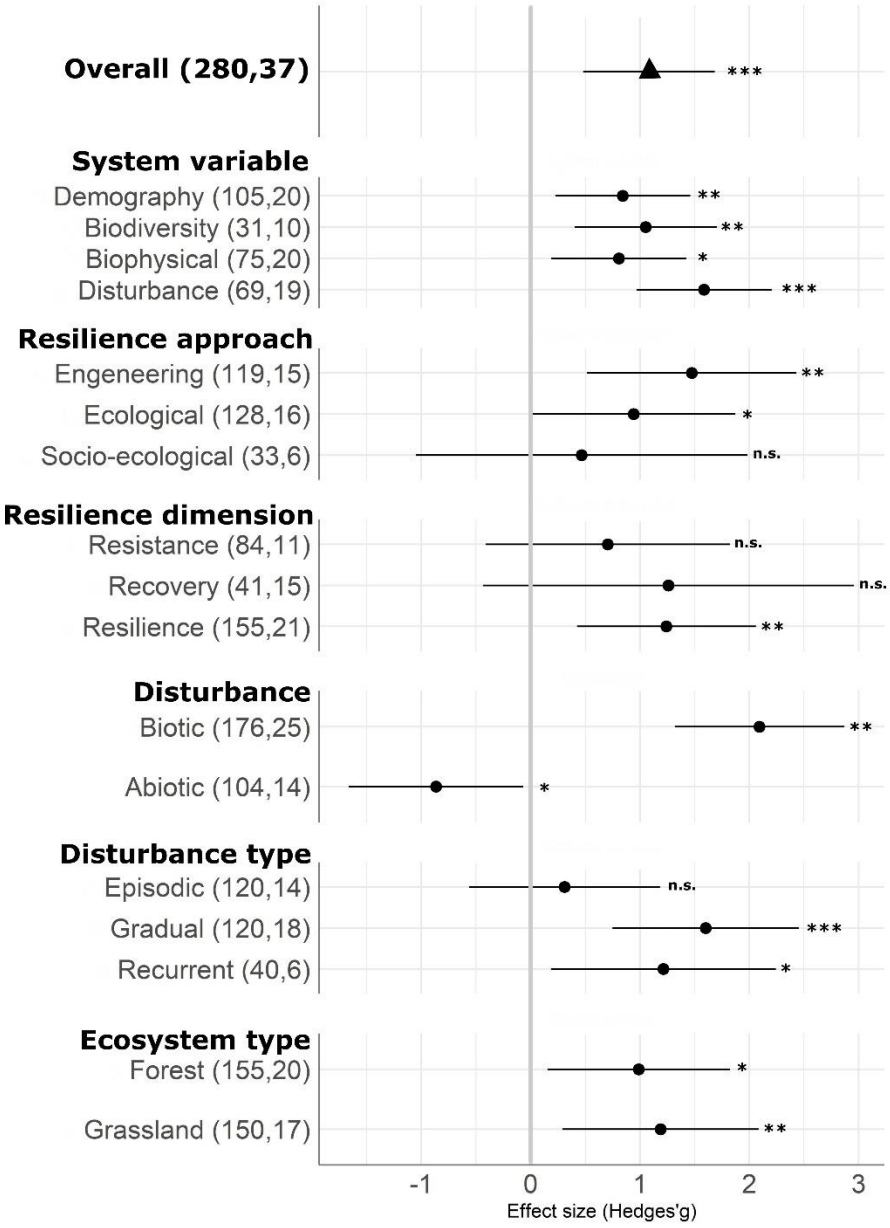


Figure 4.4. Overall effect size (black triangle) and effect size for each group of moderators (black dots) together with their confidence intervals considering all rewilding components together (biodiversity, disturbance stochasticity, and biodiversity/disturbance). Effect sizes were calculated using Hedges'g. Numbers in parenthesis indicate total number of observations and primary studies, respectively. Significant values are indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), and n.s. (non-significant See Appendix 3 Supplement S5 for the percentage of variation due to heterogeneity (I^2) and the heterogeneity among moderators (Q_M).

Overall effect sizes for biodiversity, disturbance stochasticity and biodiversity/disturbance rewilding components were positive and significant (Fig. 4.5; Appendix 3 Supplement S6) and showed high heterogeneity among observations. In addition, the meta-analysis was robust as indicated by the high Rosenthal's fail-safe number (fsnTrophic = 81,581, fsnDisturbance = 15,366, fsnTrophic/Disturbance = 15,503) showed a high value and therefore indicated robustness in meta-analysis. When considering each of the different rewilding components alone (Fig. 4.5; Appendix 3 Supplement S6), the effect size was positive and significant for all the system variables categories in exception of the group of system variables included in the biodiversity category for the biodiversity rewilding component (Fig. 4.5A), demography for the disturbance stochasticity rewilding component (Fig. 4.5B), and biophysical characteristics for the disturbance and biodiversity/disturbance components (Fig 4.5B, C).

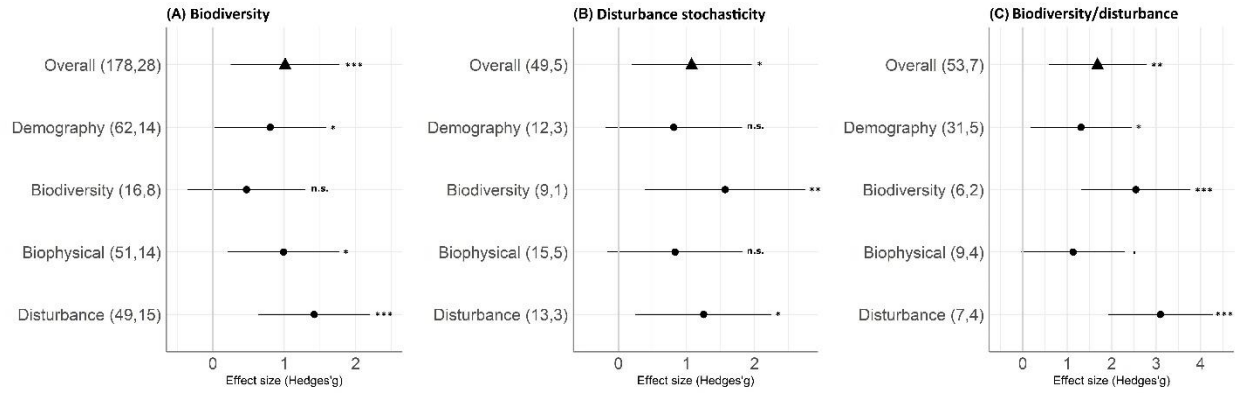


Figure 4.5. Overall effect size (black triangle) and effect size for each system variable category (black dots) and their confidence intervals for (A) biodiversity, (B) disturbance stochasticity, and (C) biodiversity/disturbance rewilding components. Effect sizes were calculated using Hedges'g. Numbers in parenthesis indicate the total number of observations and primary studies, respectively. Significant values are indicated by * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), · (<0.1), and n.s. (non-significant). See Appendix 3 Supplement S6 for the percentage of variation due to heterogeneity (I^2), and heterogeneity among moderators (Q_M).

Focusing on interventions addressing biodiversity as one of the components of rewilding most extensively covered in the literature, the overall effect on resilience was significant and positive

and showed high heterogeneity among observations (Q_{Total} = 6419.54, df = 189, P < 0.001) (Fig. 4.6; Appendix 3 Supplement S7). Furthermore, the high Rosenthal's fail-safe number (fsn = 86,013) showed a high number of observations needed to significantly change the direction of the effect size, indicating robustness of the meta-analysis. When analyzing separately each of the different biodiversity interventions alone, we found positive and significant effects for animal introduction, plant introduction, and plant removal but not for animal removal (Fig. 4.6, Appendix 3 Supplement S7).

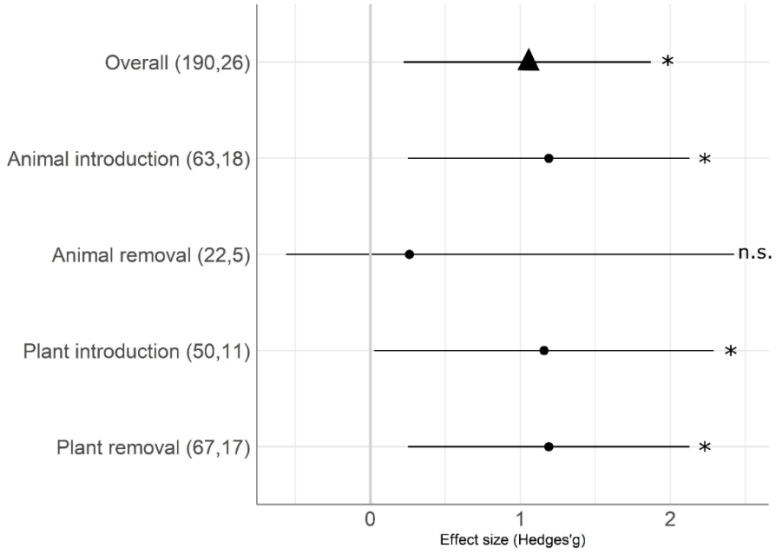


Figure 4.6. Overall effect size (black triangle) and effect size for each specific biodiversity rewilding intervention (black dots) and their confidence intervals. Effect sizes were calculated using Hedges' g. Numbers in parentheses indicate the total number of observations and primary studies, respectively. Significant values are indicated by * (<0.05) and n.s. (non-significant). See Appendix 3 Supplement S7 for the percentage of variation due to heterogeneity (I^2), and heterogeneity among moderators (Q_M).

4.5. Discussion

Our main results highlight predominantly positive outcomes of rewilding for the resilience of different system variable categories and for different types of rewilding interventions. These results support the generalized assumption that rewilding tends to enhance ecosystem resilience to climate change impacts and derived changes in disturbance regimes (Carroll & Noss, 2021; Perino et al., 2019; Svenning, 2020). Yet, we also found that rewilding does not constitute a "silver bullet" to cope with all agents and types of disturbances, as it may have neutral effects or even fail. According to our results, rewilding interventions exhibited lower resilience in front of abiotic disturbances such as drought and showed no effects for episodic disturbances. Ultimately, this does not overturn the overall reported benefits of rewilding but highlights the complexity and context-dependence of its outcomes (Torres et al., 2018) and the eventual need to apply accompanying measures. Particularly, this can be the case of rewilding projects with a strong emphasis on restoring pre-disturbance characteristics which may not be the most suitable ones in a time of intense climate change, as suggested by the fact that most negative outcomes observed correspond to studies addressing engineering resilience. Despite the potential interest of our results which stem from a meta-analysis based on a conservative selection of articles including observational and experimental data - mostly collected decades after rewilding took place - these should be interpreted with certain caution as the number of studies assessed was relatively limited.

Notwithstanding the growing attention towards rewilding approaches to restore biodiversity and foster the adaptation to climate change by recovering natural ecosystem processes, we did not find any primary case studies targeting simultaneously all three rewilding components proposed by Perino et al. (2919). In addition, a clear underrepresentation of the dispersal (i.e., connectivity) component suggests that little attention has to date been paid to this ecological function in rewilding initiatives. This is an important finding as many species may critically depend on connectivity among habitats to enhance the recovery of their populations following disturbances by allowing gene flow and recolonization opportunities (Rey Benayas & Bullock, 2015; Selwyn et al., 2023). Overall, future research would welcome the assessment of rewilding interventions over a more comprehensive view of interacting natural processes in order to allow appreciating the relative role of the recovered processes and their interactions with already existing ones on ecosystem resilience.

Our vote-counting results demonstrated that a high proportion of observations reported a positive effect of all rewilding components on resilience (68.20%), and this result was also confirmed by the meta-analytical approach (Figs. 4.3 and 4.4). However, we point out that 11.80% of observations reported neutral effects, and 20% reported negative effects, emphasizing the abovementioned intricate and context-specific characteristics of rewilding initiatives (Torres et al., 2018). The highest proportion of negative outcomes of rewilding for enhancing resilience was reported for the biodiversity (i.e., trophic complexity) component and mostly corresponded with unexpected undesirable effects of plant and animal introductions (Fig. 4.3). For these same cases, our results also pointed out a significant failure of rewilding for the resilience to abiotic disturbances (Fig. 4.4). Interestingly, these results were associated with a poorer response to extreme fire and drought events, suggesting that rewilding efforts aiming to enhance trophic complexity (e.g., predator-prey interactions, herbivore introductions) may fall short to buffer ecosystems against severe climatic events. Thus, although functional diversity has been reported to potentially increase resilience to drought events (Grossiord, 2020), the demographic weakness of the reintroduced species during the initial stages may be severely impacted by drought, disrupting trophic interactions, and destabilizing the whole ecosystem (Martínez-Vilalta et al., 2011). In support of this reasoning, we found that most negative effects were related to impacts within the category of demography-related system variables (Fig. 4.3B) such as density and survival (e.g., Blumroeder et al., 2022). Moreover, the vote counting analysis indicated that observations reporting negative effects of rewilding on resilience mostly corresponded to studies focused on an engineering resilience approach (i.e., returning to the pre-disturbance ecosystems); this suggests that the species composition and structure promoted by rewilding might lack the adaptive flexibility required to cope with rapidly changing abiotic conditions (Merlin et al., 2015). This lower flexibility can result from the lack of appropriate reference ecosystems or an excessive focus of rewilding projects on restoring historical conditions, which may not be able to handle new and intensified abiotic disturbances rising from climate change (i.e., extreme fire or drought events; Blumroeder et al., 2022). On the contrary, our results showed a major positive effect of rewilding on resilience to disturbances driven by biotic agents (Fig. 4.4), such as pests and, particularly, biological invasions. These results suggest that biotic feedbacks (e.g., herbivory) may provide high regulation against biotic-driven disturbances to counterbalance changes in the

ecosystem, contrary to abiotic disturbances which are beyond the control of the biotic components of ecosystems (Blumroeder et al., 2022; Mungi et al., 2023).

Our meta-analysis generally revealed positive and significant effects of rewilding for engineering and ecological resilience, but non-significant effects for socio-ecological resilience (Fig. 4.4). This might be because socio-ecological systems are influenced by a broader range of social, economic, and cultural factors (Folke, 2006) that were not specifically targeted in the primary studies (De Pascali et al., 2024; Staab et al., 2015) or included as moderators in our meta-analysis, indicating that more integrated approaches are needed when implementing rewilding actions with specific social objectives in mind. In the same line, when analyzing resilience dimensions, the non-significant effects when considering resistance and recovery separately but the positive effects for resilience, point out that the positive effects of rewilding may become more apparent when considering a holistic dimension of resilience rather than its isolated components (Fig. 4.4). Although this statement should be interpreted with caution as it may stem from an insufficient sample size, it is supported by the fact that 70% of our rewilding case studies reported positive effects when analyzing the overall resilience dimension.

Regarding the characteristics of the restored ecosystem, the vote counting analysis indicated that the resilience of the biodiversity system variable was almost universally enhanced by rewilding (Fig. 4.3B). A large amount of these positive biodiversity observations in the vote counting analysis (Fig. 4.3B) were mostly linked to the biodiversity rewilding component, particularly through interventions like wild or domestic herbivore introductions or invasive plant removal which effectively mitigate the primary disturbance type (i.e., plant invasions). Some of our primary studies showed that by preferentially grazing on invasive species, herbivores may help to maintain or restore the native plant community structure and control future invasions by alien species, thus enhancing biodiversity resilience (Kapas et al., 2020; Mungi et al., 2023). Similarly, removing invasive plants directly contributes to biodiversity by eliminating species that negatively impact native ones and helps to reinforce biodiversity (Wright et al., 2021). However, when considering the meta-analytical approach, two cases reporting negative effects for grassland resilience to invasive species (Assis et al., 2021; Cava et al., 2018) derived in contrasting results for the biodiversity system variable when targeting the biodiversity rewilding component as these were not significant (Fig. 4.5), stressing once more the context-dependency in the outcomes of

restoration practices. Interventions targeting disturbance stochasticity and biodiversity/disturbance rewilding components also significantly increased resilience of the biodiversity system variable category, by for instance mimicking the effects of traditional livestock grazing, which caused an increase in native species composition (Tardella et al., 2020; Fig. 4.5). Restoring and preserving biodiversity have been identified as crucial for ecosystems to face uncertain and increasingly disturbed ecological scenarios, as biodiversity has been observed to be the main driver in enhancing the resilience of ecosystems, with cascading positive effects through the whole network of system variables (Hurtado et al. under review; Kunming-Montreal Global Biodiversity Framework). Indeed, more diverse ecosystems may be better equipped to withstand and recover from disturbances, by increasing the range of potential responses and providing functional complementarity that fosters the efficient use of resources (Jactel et al., 2017; Messier et al., 2022).

4.6. Conclusions

Overall, this research has shown that rewilding actions aiming towards increasing biodiversity and disturbance stochasticity were globally effective in increasing ecosystem resilience by enhancing (i) individual characteristics and demographic processes, (ii) compositional, trophic and functional biodiversity, (iii) biophysical characteristics and structure, and (vi) characteristics of the disturbance regime. Yet, specific factors such as the resilience approach and dimension, the disturbance agent, and the nature of the interventions practiced played crucial roles in determining the outcomes of rewilding for resilience. Ultimately, this highlights that, despite generally providing positive results, the outcomes of rewilding are often context-dependent and may eventually require complementary interventions to play out their full strengths.

Chapter 5 -
General Discussion

Under the current biodiversity and climate change crisis there is a growing interest in restoring degraded ecosystems worldwide to address the challenges imposed by climate change and related disturbances (Bellard et al., 2012). In this context, assessing the role of trophic interactions in ecosystem restoration may be crucial, as these play a fundamental role in maintaining ecosystem structure, function and stability (e.g., Forup et al., 2008; Ribeiro da Silva et al., 2015). However, understanding the role of trophic interactions for ecosystem restoration and how it may be affected by several factors (e.g., functional traits, environmental conditions), or whether the desired outcomes are achieved remained seldomly assessed to date. Thus, the main contribution of the present thesis deals with these issues by investigating the role of trophic interactions for forest restoration success, the factors that influence the recovery of tree species diversity, and whether resilience is being accomplished in rewilding efforts. We found that trophic interactions play a crucial role for forest restoration and biodiversity recovery and that targeting them in restoration efforts generally increases ecosystem resilience. Moreover, we revealed the interplay between species' functional attributes (e.g., seed size, shade and drought tolerance) and the environmental context (i.e., connectivity, management, climatic conditions), which determines the outcomes of forest restoration success and resilience (Fig. 5.1).

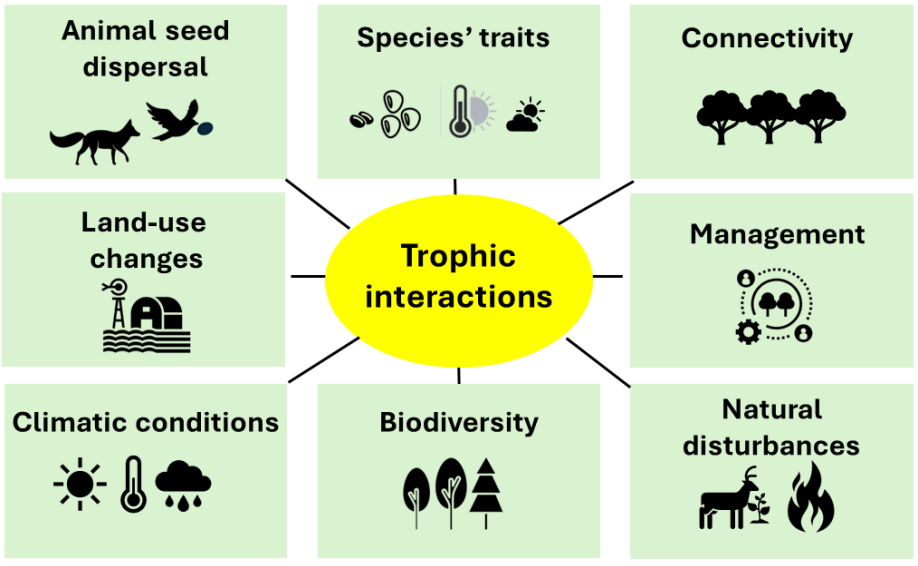


Figure 5.1. Main factors determining the role of trophic interactions for forest restoration and resilience.

The role of animal seed-dispersal on successful restoration

The first question addressed in this thesis (Q1) explored whether there was a differential contribution of intrinsic and extrinsic factors influencing animal-seed dispersal for forest restoration success across biomes. As so, we have documented that several factors related to plant dispersal syndromes and seed dispersal traits, together with the ecological and environmental conditions modulated the success of recovery efforts by determining seed arrival and establishment (Chapter 2). Specifically, we revealed that the main factors affecting restoration success were the extrinsic ones (i.e., fragmentation and type of restoration conducted) (Wolfe et al., 2019), while species richness and abundance and the ability of animals to achieve long-distance dispersal were the main intrinsic factor (Schupp et al., 2019). Regarding differences among biomes, we observed that for extrinsic factors, especially for the restoration approach, more intense efforts seem to be needed in tropical systems (i.e., reconstructive restoration) while assisted restoration (i.e., perch placements) was enough for temperate systems (Gann et al., 2019). Whitin intrinsic factors, rodent frugivory and large-sized seeds were related to unsuccessful restoration in tropical forests (Galetti et al., 2015), while frugivory by carnivores and small-sized seeds favored restoration in temperate ones, highlighting ungulate frugivory as the main constrain to restoration in this biome (Selwyn et al., 2020). Therefore, understanding the interplay between these intrinsic and extrinsic factors influencing the seed dispersal process in different biomes will be essential for applying effective restoration strategies (Tylianakis et al., 2010).

Regarding landscape features, our study corroborates that habitat fragmentation poses a threat to forest restoration success by limiting the movement of seeds into restoration sites (Chapter 2), halting the recovery of populations by disrupting movement pathways (Cote et al., 2017). Contrarily, habitat connectivity proved to be of paramount importance for passively increasing tree diversity in the Mediterranean forests investigated in Chapter 3, specifically for the recruitment of those tree species dispersed by animals. Such result is line with the general benefits attributed to connectivity emphasized in previous studies (Auffret et al., 2017; Cote et al., 2017). However, although the general benefits of connectivity for dispersal have been repeatedly claimed, specifically for allowing the recovery of populations following disturbances (Rey Benayas & Bullock, 2015), we found a clear underrepresentation of this component in the literature related

with rewilding (Chapter 4). This finding suggests that more research is needed on this topic to better address the benefits of dispersal functions for resilience.

Within factors related to the dispersal capacities, we found that the abundance and diversity of frugivorous animals as well as fruit resource availability chiefly contributed to restoration success (Chapter 2). This result highlights that the variety and availability of seeds and seed dispersers are crucial for transporting seeds into restoration sites, determining the potential for a diverse plant community, and ultimately for establishing resilient ecosystems (Vander Wall & Beck, 2012). Additionally, in Chapter 4, we disclosed that the demographic (i.e., abundance, density) and biodiversity (i.e., richness, Shannon diversity index) system variables assessed in rewilding projects contributed to higher resilience to disturbances, manifesting the importance of such variables for coping with the uncertainty posed by increasing climate change and related disturbances (Carter & Blair, 2012; Gordon et al., 2021). Thus, promoting abundance and diversity by different means (e.g., planting tree mixtures) is particularly important not only for enhancing ecosystem restoration, but also for enhancing ecosystem resilience (Jactel et al., 2017; Messier et al., 2022a).

Interestingly, from the plant's perspective, seed size is supposed to be the most relevant trait for seed regeneration: large-sized seeds are better adapted to adverse biotic and abiotic factors, including competition, drought, and nutrient limitations (Muñoz et al., 2017). However, large seeds require large animals to transport them, and these are becoming less abundant worldwide and may limit the opportunities for long-distance seed dispersal (Wotton & Kelly, 2012). In this sense, consistent with the results of previous studies (Markl et al., 2012; Menke et al., 2012), we found that large-sized seeds were more often associated with unsuccessful restoration outcomes in tropical forests (Chapter 2). Likely to extreme hunting pressure of large frugivorous mammals and birds responsible to disperse large seeds in these habitats, it has been warned that such disruption of these seed dispersal interactions can cause changes in species composition in tropical forests, leading to compositional homogenization by small-seeded tree species (Markl et al., 2012; Wotton & Kelly, 2012). Thus, we advocate for the protection and conservation of specialized large animal seed dispersers (e.g., primates and ungulates) for improving the regeneration of tropical forests. Contrarily, a more generalist array of seed dispersers may be promoted in temperate systems, as we found that small and medium sized seeds, which are dispersed by a greater assemblage of birds

and small mammals (Fedriani et al., 2018; González-Varo et al., 2019), were related to higher restoration success in temperate forests (Chapter 2).

Determining which type of restoration approach is to best apply may depend on several factors, such as historical conditions, degree of degradation, or ecological goals (Clewell & Aronson, 2012). Regarding active restoration strategies, our results indicate that assisted restoration actions (e.g., perch placements) would be often enough for temperate systems while more reconstructive efforts (e.g., active tree planting) would be needed in tropical ones, suggesting that human intervention might be required to accelerate forest regeneration in areas which might have been highly disturbed (Holl, 2017; Mittelman et al., 2020). Contrarily, the negative outcomes for passive recovery in temperate systems, highlights that several limiting factors (e.g., seed predation, intense herbivory, stressful abiotic conditions) may impede restoration mediated by seed dispersal functions when no actions are conducted (Chapter 2). Although this type of restoration has been recommended as a considerably cheaper alternative, this outcome should be taken into consideration, specifically under the context of land use change which is particularly evident in some temperate systems (e.g., Mediterranean) (Palmero-Iniesta et al., 2020) and therefore some restoration actions may be required. Somehow, these results suggest the advantages of active against passive strategies for which restoration objectives need to be examined to select the best practices. Finally, we suggest that long-term monitoring and evaluation of restoration actions will be essential to provide higher quality for restoration assessments, as the effects of short-term timeframes have proved to less contribute to restoration success.

The role of dispersal, land use changes, management release and climate on increasing tree species diversity

Our second question (Q2) addressed the different environmental and forest management factors, together with species functional traits triggering passive changes in tree species diversity. As so, in Chapter 3 we found that tree species diversity has passively increased in Catalan forests after a period of ca. 30 years mostly influenced by the release of intensive forest management, the changes in climatic conditions, and by the significant role that animal-mediated seed dispersal and some particular species traits (i.e., drought tolerance) played. Here we revealed how the increase in

temperatures and decrease in precipitation favored the recruitment of animal dispersed and higher drought tolerant species, highlighting the importance of dispersal in enabling species to track climate fluctuations and environmental change (Corlett & Westcott, 2013). Interestingly, this result is in line with other studies reporting similar shifts in tree species diversity mainly driven by the effects of climate (e.g., Vayreda et al., 2016; Sánchez de Dios et al., 2023) and may be critical to enhance resilience in such forests under increasing arid conditions derived from climate change (García-Valdés et al., 2021).

Remarkably, the reported passive tree diversity increase could be considered as an indicator of successful forest recovery. In this sense, numerous studies have emphasized the advantages of enhancing tree species diversity (Jactel et al., 2017; Messier et al., 2022a) as it is expected to increase the range of species responses to disturbances, ensuring that species will continue to function even when others fail (Yachi & Loreau, 1999). Considering that recent and long-established forest in the area currently exhibit similar tree species richness and diversity (Basnou et al., 2016; Cruz-Alonso et al., 2021), the reported increase seems to stem from the recovery of long established forest after the cessation of intensive management in the last decades (Espelta et al., 2020).

Moreover, we also found negative effects of recent forest management, which could be caused by delivered biased harvesting of particular tree species or undesired effects of forest harvesting operations for the regeneration layer (e.g., trampling), showing the need to tailor restoration strategies aimed at enhancing diversity in secularly disturbed forests. In this line, the debate between shifting to strict conservation or maintaining forest exploitation represents two contrasting approaches to forest management which may pose significant socio-ecological implications (Sjölund & Jump, 2013). Balancing these approaches could include shifting the exploitation towards more recently established and highly productive forests which could encourage the restoration process in long-existing forests where secular forest management lowered tree species diversity (Puettmann et al., 2015). In addition, we suggest tailoring silvicultural practices towards biodiversity conservation (e.g., close to nature forestry) to overcome the negative consequences of recent forest management for tree species diversity. Also, future conservation strategies should consider that climatic conditions are changing (Corlett & Westcott,

2013), and thus it will become a priority to identify which species, functions and ecological processes can overcome such threats to adequately apply the right conservation strategy.

Changes in climatic conditions such as the increase in temperature and the decrease in precipitation observed in our study sites in Catalonia, also modulated tree species diversity changes (Chapter 3). Regarding the key functional traits mostly contributing to driving changes in tree species diversity we found that animal dispersed species and those more adapted to drought led the increase in tree species diversity. Thus, promoting a greater presence of such highly mobile species may improve the capacity of forests to surmount ecological filters posed by increasing climate change disturbances in the future (Corlett & Westcott, 2013). Although we observed a general increase in tree species diversity, the increase for the tree layer was lower in forests that experienced higher warming, while the opposite situation was observed for the regeneration layer. The patterns observed for the tree layer could be related to the impact of tree decay and mortality episodes documented in the region in areas that are experiencing general warming and are occupied by more drought sensitive species (e.g., *Pinus sylvetris, Fagus sylvatica*) (Chaparro et al., 2017). Contrarily, we also found that mediterranean-drought adapted species (e.g., *Quercus* spp.) in the regeneration layer boosted their recruitment under such warming conditions, indicating they benefit from the opportunities arising from the gaps created due to tree mortality (Espelta et al., 2011).

The increase in tree species mixtures reported in this thesis may have important implications for forest functioning by enhancing productivity and resilience to disturbances (Jactel et al., 2017). However, in contrast to more classical succession theories, which often predict a gradual shift from pioneer to late successional species, our results suggest that mixed conifer-broadleaf forests might represent a stable, long-term alternative successional scenario under the current effects of climate warming. This stability could arise from the adaptative advantages of maintaining diverse species composition, which may be better equipped to cope with the unpredictable environmental conditions expected in the future. Thus, fostering mixed species forests could become crucial for enhancing the resilience of forests by ensuring ecosystem complementarity under changing climatic conditions (Sánchez de Dios et al., 2023).

Does rewilding increase ecosystem resilience to disturbances?

The thesis also provided some interesting insights regarding the potential role of rewilding initiatives on restoring ecosystem functioning and especially the role of their main rewilding components (i.e. trophic complexity, stochastic disturbances and dispersal) for increasing resilience to disturbances (Q3). Although in Chapters 2 and 3 we demonstrated the general benefits of seed and propagule dispersal for forest recovery, it seems that somehow this process is underrepresented in rewilding efforts (Chapter 4). This could be because measuring dispersal and tracking dispersers is notoriously challenging, but ongoing advancements in existing methods and the development of new techniques are steadily improving our capabilities (Tesson & Edelaar, 2013). However, further research is needed to deepen our understanding of dispersal processes and to enhance our ability to predict ecosystem responses in the face of accelerating global change. Moreover, we did not find any case studies which targeted the three rewilding components (i.e., trophic complexity, disturbance stochasticity and dispersal) simultaneously and thus, we advocate that the three rewilding components should be targeted simultaneously in order to fully target ecosystem recovery (Perino et al., 2019).

Our main results highlighted mostly positive outcomes of rewilding for the resilience of demographic processes, biodiversity, biophysical characteristic and characteristics of the disturbance regime supporting the general assumption that rewilding tends to enhance ecosystem resilience to climate change impacts (Carroll & Noss, 2021; Perino et al., 2019; Svenning, 2020). However, rewilding is not a one-size-fits-all solution, as we found that it may sometimes fall short, for instance, when addressing abiotic disturbances or for the resilience of socio-ecological systems. Specifically, in Chapter 4 we found that trophic rewilding interventions (e.g., plant or animal introductions or removal) did not always enhance resilience under abiotic disturbances (e.g., drought, fire). These findings suggest that efforts to increase trophic complexity alone may be insufficient to buffer ecosystems against severe climatic events. Thus, although higher functional diversity has been reported to potentially increase resilience to drought events (Grossiord, 2020), the demographic vulnerabilities of the reintroduced species may be exacerbated by drought, leading to disrupted trophic interactions, and destabilizing the entire ecosystem (Martínez-Vilalta et al., 2011). Supporting this view, we observed that most negative effects were associated with demographic variables, such as population density and survival rates which were particularly

impacted under these stressors (e.g., Blumroeder et al., 2022). Moreover, as most of these studies corresponded to the so called *engineering resilience* (i.e., the recovery of a system to its previous undisturbed state (reference state); Pimm, 1984), this could suggest that the species composition and structure promoted by rewilding might lack the adaptive flexibility required to cope with rapidly changing abiotic conditions (Merlin et al., 2015). This lack of flexibility can stem from the focus on restoring historical ecosystems, which may not be equipped to handle new and intensified abiotic disturbances brought about by climate change and human stressors (i.e., extreme fire and drought events) (Blumroeder et al., 2022). For instance, in such systems, natural disturbances are often suppressed (e.g., fire suppression) which may lead to larger and more devastating disturbance events (e.g. large wildfires instead of smaller and more frequent ones) hindering the natural regeneration potential and reorganization process (Perino et al., 2019). In this sense, in Chapter 4 we found that rewilding actions aimed at recovering stochastic disturbances by reducing the continued anthropogenic control enhanced the recovery of ecosystems attributes under new abiotic disturbances (e.g., Hood et al., 2016; Stephens et al., 2024). In similar lines, in Chapter 3 we found that following intense management release, the region seems to be shifting towards an increase in tree species diversity even under the context of increasing aridity. If such management may be replaced by a more natural disturbance regime, the observed pattern could also be explained by the role that stochastic disturbances (i.e., drought, fire, pests) may play for supporting biodiversity by, for instance, preventing competitive exclusion allowing for greater species coexistence (Hamilton & Burton, 2023). Thus, under increasing abiotic disturbances, focusing restoration efforts to adaptative management strategies which target disturbance stochasticity could help to better cope with the uncertain conditions posed by climate change under such events.

Additionally, we revealed that rewilding did not show significant effects within the context of socio-ecological resilience. This may be due to the complex nature of socio-ecological systems, which are shaped by a wide array of social, economic and cultural factors that were not specifically addressed in the primary articles analyzed (e.g., De Pascali et al., 2024; Staab et al., 2015). More integrated approaches when addressing rewilding actions are needed as these systems require more than just ecological interventions, as human behaviors, governance structures, and economic dependencies could also play critical roles in their resilience (Folke, 2006). To effectively enhance socio-ecological resilience through rewilding, it is essential to adopt more integrated approaches that encompass both ecological and socio-economic dimensions. This means incorporating

interdisciplinary research, engaging local communities, and considering the socio-economic impacts of rewilding projects. By doing so, rewilding efforts can be better tailored to address the specific needs and challenges of socio-ecological systems, potentially leading to more sustainable and equitable outcomes. Without such integration, rewilding initiatives may fall short of their potential to contribute meaningfully to both ecological and human well-being (Folke, 2006).

Future perspectives

Some uncertainties remain in this thesis regarding the underlying mechanisms and drivers of forest restoration and resilience influenced by trophic interactions. The intricacy of this topic, coupled with the unique characteristics of each study system, poses a significant challenge in identifying key determinants and drawing generalized conclusions when addressing the factors underpinning ecosystem recovery and resilience. Although this thesis provides valuable information for practical applications in forest restoration under changing global conditions, our findings suggest that to accurately assess the role that trophic interactions may have for ecosystem restoration and resilience, further research is needed on this topic.

Specifically, additional research will be essential to deepen our understanding of the dispersal processes and improve our ability to predict how ecosystems will respond to the accelerating pace of global change. Animal-mediated seed dispersal has proved to have important implications for forest regeneration by allowing species to colonize new areas, escape unfavorable conditions, and maintaining biodiversity (Chapters 2 and 3). However, the exact mechanisms and patterns of dispersal are still not fully identified and understanding whether or how the dispersal processes may vary across different environmental conditions will be of paramount importance under the context of climate change. Some studies have documented the critical role of dispersal for tracking climate fluctuations (e.g., Corlett & Westcott, 2013), but to date the implications that the dispersal process may have for ecosystem resilience still remains unaddressed, as highlighted by the null representativeness obtained for the dispersal rewilding component in rewilding efforts (Chapter 4). Moreover, it is acknowledged that climate change may also pose a threat to seed dispersal functions by disrupting species' movements and thus may markedly reduce the capacity of many plant species to track shifts in suitable habitat under climate change (Mokany et al.,

2014). Accordingly, further research should focus on understanding how the distributions of species may shift under climate change through model projections and long-term observations.

As climate change is rapidly altering environmental conditions it will be important to contribute to fostering the resilience of forests to improve their resilience under unpredictable conditions expected in the future. In this sense, increasing biodiversity could become crucial for enhancing resilience by ensuring ecosystem complementarity under changing climatic conditions (Sánchez de Dios et al., 2023). As stated in this thesis, several factors seem to influence the recovery of biodiversity in Catalan forests (Chapter 3). However, we support that further research should focus on certain management strategies that could enhance biodiversity of forest ecosystems. In this sense, diverting forest management towards more recently established and highly productive forests could alleviate the pressure on long-established forests, where historical management practices have often led to a decline in tree species diversity (Puettmann et al., 2015), allowing these long-existing and long-exploited forests to undergo natural restoration. At the same time, by prioritizing in such management the tree specific species traits that are most likely to withstand these environmental shifts, can better tailor conservation efforts to withstand the impacts of changing climatic conditions.

Finally, we propose that enhancing ecosystem resilience to climate change and related disturbances can be achieved by advancing research on more integrated rewilding approaches. These approaches should simultaneously address the three key components of rewilding (i.e., trophic complexity, disturbance stochasticity, and dispersal) alongside the two primary dimensions of resilience: resistance and recovery. Our research indicates that rewilding generally offers benefits in coping with biotic disturbances. However, it faces challenges in addressing abiotic disturbances, such as those outlined in Chapter 4. Given that climate change is likely to increase the frequency of events like fires and droughts, it is crucial to develop effective strategies for managing these abiotic threats. Our findings suggest that placing a stronger emphasis on the disturbance component of rewilding could improve responses to abiotic disturbances. Nonetheless, additional research is needed to fully understand the effects of stochastic disturbances on ecosystem resilience, despite ongoing efforts in this area (e.g., Hood et al., 2016; Stephens et al., 2024).

General Conclusions

Chapter 2

1. Animal-mediated seed dispersal is a key process to ensure forest restoration success in both tropical and temperate biomes. However, differences among biomes in the importance of intrinsic and extrinsic dispersal factors influencing seed dispersal must be considered to specifically apply adequate restoration strategies regionally: it seems that assisted restoration efforts (e.g., perch placements) are enough for restoring temperate forests while reconstructive (e.g., active planting) efforts are more necessary in tropical ones.

2. Plant dispersal syndromes and seed dispersal traits are the most relevant intrinsic factors determining restoration success stressing the importance of actions to ensure their matching. Specifically, accounting for the diversity and abundance of animal seed dispersers as well as fruit resource availability should be considered when planning restoration actions.

3. Within environmental factors, landscape features such as connectivity and habitat quality need to be ensured to favor animal movements into restoration sites as the lack of propagules could impede restoration of taxonomic and functional diversity. Also, considering microenvironmental conditions where seeds are deposited will be of major importance as stressful conditions (e.g., high light and temperature) could limit survival and growth once seeds have reached restoration sites.

Chapter 3

1. After almost 30 years tree species richness and diversity has passively increased in NE Iberian forests, mostly influenced by land use changes and the release of intensive forest management. To maintain and further enhance this diversity, it will become crucial to adopt specific measures that promote silvicultural practices tailored towards biodiversity conservation (e.g., close to nature forestry) and shifting management towards more recent and productive forests.

2. Changes in tree species diversity also appear to be influenced by climatic trends, such as rising temperatures and decreasing precipitation. These changes have led to the opportunities for seedling recruitment in those forests experiencing tree decay and mortality due to intense drought events. In particular, the establishment of species with high drought tolerance has played

a key role in contributing to the mixed character of Catalan forests. This suggests that these drought-tolerant species may become increasingly important for enhancing forest resilience as aridity is expected to intensify due to climate change.

3. Animal seed dispersal played a significant role in increasing tree species diversity. It was particularly important for facilitating the arrival of new species from the regional pool. Connectivity between habitats was crucial in this process, and therefore, maintaining and improving connectivity is essential for enabling tree species to track changing environmental conditions.

Chapter 4

1. Most rewilding projects aim at recovering trophic complexity or disturbance stochasticity, while the dispersal component is underrepresented, highlighting a gap in addressing this crucial ecological function to ensure resilience and the lack of holistic approaches in rewilding projects.

2. Rewilding interventions generally proved to enhance resilience of demographic processes, biodiversity, biophysical characteristics and disturbance characteristics under different disturbance types. By conducting specific interventions, such as herbivore introductions or invasive plant species removals, resilience to biotic disturbances was enhanced by maintaining native plant community structure and controlling invasive species.

3. Although mostly positive, rewilding also resulted in mixed effects on ecosystem resilience, showing both neutral and negative outcomes. Particularly in response to abiotic disturbances like drought and fire events, emphasizing the context-dependent nature in the outcomes of rewilding efforts and its potential limitations, particularly when the aim is to recover the historical ecosystems. Also, when it comes to enhancing socio-ecological resilience, these findings suggest the need for more integrated approaches that also address social factors.

Appendix 1

Supplementary material – Chapter 2

SUPPLEMENT S1: Number of publications by biome, continent, and country and geographic representativeness of the study area.

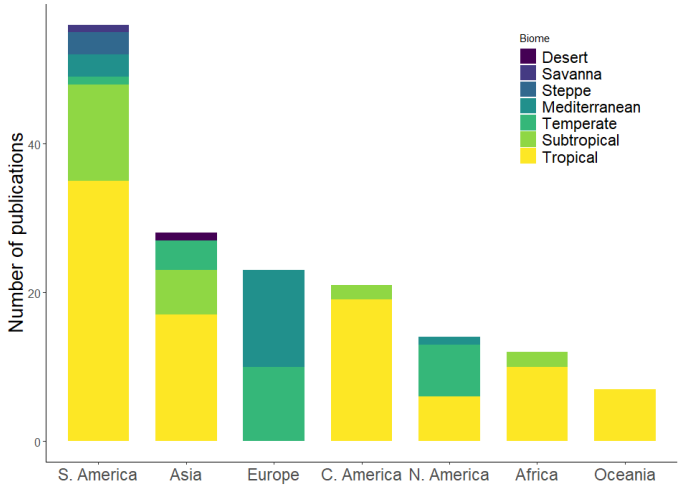


Figure S1.1. Total number of publications by continent and type of biome.

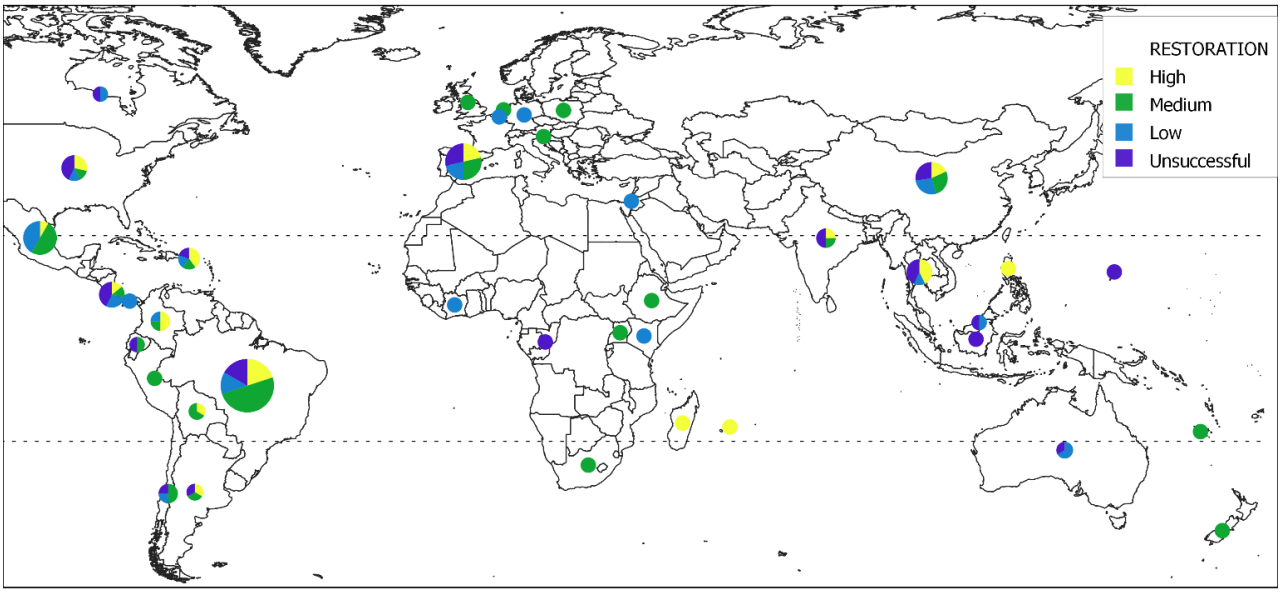


Figure S1.2. Global distribution of case studies assessing forest restoration by means of seed dispersal functions. Pie charts provide data on seed dispersal effectiveness in forest restoration for each country. Pie chart size represents total numbers of case studies in each country. Dash lines represent the Tropics of Cancer and Capricorn. Also, the geographic representativeness of the

overall restoration success showed that Tropical and Subtropical regions represent most of the case studies and the highest number of highly successful and unsuccessful restoration outcomes. Whereas Mediterranean and Temperate regions showed a lower number of case studies and a medium success outcome.

Table S1.1. Number of publications found by country.

Country	N publications	Country	N publications
Argentina	3	Malasya	2
Australia	3	Mariana archipielago	1
Belgium	1	Mauritius	1
Bolivia	3	Mexico	13
Brazil	35	Netherlands	1
Canada	2	New Caledonia	1
Chile	4	New Zealand	2
China	12	Panamá	1
Colombia	4	Perú	2
Congo	1	Philippines	1
Costa Rica	10	Poland	1
Ecuador	2	Puerto Rico	5
Ethiopia	2	Rwanda	1
Germany	2	Scotland	1
India	4	Slovenia	1
Indonesia	1	South Africa	1
Israel	1	Spain	16
Ivory Coast	1	Thailand	7
Kenia	1	Uganda	2
Madagascar	1	United States	7

SUPPLEMENT S2: Description of variables.

DOI: Reference information for the study.

Publish year: Year of publication for each study.

Country and continent: Geographical location of the study.

Biome: Tropical, Temperate, Mediterranean, Desert, Steppe or Savanna. Each forest was classified based on the geographic position of the study site using the global Köppen-Geiger climate classification map (http://koeppen-geiger.vu-wien.ac.at/present.htm).

Forest protection type: To be consistent between different countries' protection categories (e.g., Wildlife Reserve, National Forest, Ecological Park), we standardized forest protection into Protected, Unprotected and Experimental Site.

Disturbance categories: Past land use or disturbance for each study site (agriculture (crops), mines, game, landfill, fire, natural disturbance, presence of alien species, pasture (grazing), urbanization) and its ultimate effect on the study site: i) "deforestation" (degree of absence of forest cover); ii) "fragmentation" (distribution of forest area in discontinuous forest patches); and iii) "defaunation" (absence of animal dispersers either in fragmented or deforested sites). Disturbance categories were not mutually exclusive for the study sites.

Initial conditions: initial conditions of the study sites reported in each primary study at the time when the restoration assessment took place has been used as a proxy of the degree (severity) of forest disturbance. According to the information available, this variable has been categorized into "highly degraded" sites (i.e., the primary articles reported highly degraded sites with extensive fragmentation, presence of alien species, low plant and animal dispersers richness and abundance) and "least degraded" sites (i.e., the primary articles reported least degraded conditions, including the remaining of forest cover in the area, the presence of native forest and animal dispersers species).

Management age: Number of years since restoration has taken place or since the land use ceased and forest recovered without further human intervention in each study site.

Plant richness and abundance: Metrics measured in the primary studies. In these studies, abundance measures could include vegetation biomass, counts or percentage of individuals and

cover. Diversity measures included species richness and evenness. These two metrics were categorized into "high" (when according to the authors of the primary studies, vegetation cover and diversity was estimated to be in adequate levels in each study site), "medium" (when vegetation cover and diversity was estimated to be in adjusted levels in each study site) and "low" (when vegetation cover and diversity was estimated to be in insufficient levels in each study site).

Animal disperser richness and abundance: Metrics measured in the primary studies. In these studies, the abundance measure included faunal (potential animal seed dispersers) counts or degree of occupancy of the study site. Diversity measures included species richness. These two metrics were categorized into "high" (when in the primary studies, occupancy or diversity was estimated to be in adequate levels in each study site), "medium" (when occupancy or diversity was estimated to be in adjusted levels in each study site) and "low" (when occupancy or diversity was estimated to be insufficient levels in each study site).

Restoration approach (management type): Categorized into: a) Passive, b) assisted (active) or c) reconstructive (active) for both animal dispersers and plants.

Animal protection: Protection status of each animal disperser that appears in each of the studies (least concerned, threatened, endangered).

Frugivory type: Mammal or bird frugivory. Mammal order. Generalist or legitimate dispersal.

Seed size: Each potentially dispersed plant species' seed size (i.e., longest axis of the seed) assessed in the primary study. We categorized this metric in "small" (<5mm), "medium" (5-10mm) or "large" (>10mm) sized seeds according to the literature (Levey 1987; Verdú & Traveset 2004; Fuzessy et al. 2018).

Levey DJ (1987) Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist*, 129(4), 471-485

Verdú M, Traveset A (2004) Bridging meta-analysis and the comparative method: a test of seed size effect on germination after frugivores' gut passage. *Oecologia*, 138(3), 414-418

Fuzessy LF, Janson, C, Silveira FA (2018) Effects of seed size and frugivory degree on dispersal by Neotropical frugivores. *Acta Oecologica*, 93, 41-47

Hoarder activity: Animal's hoarder behavior.

Embedded trophic interactions: Animal dispersers were also involved in other interaction types (pollination, predation, insectivory or granivory).

Animal seed dispersal distance ability (SDD): Categorized into **"**short", "medium" or "long", for each animal disperser following an estimated SDD provided by Jones et al. 2017's literature review.

- Short: usually achieved by small-sized mammals such as rodents (SDD < 100m).

- Medium: usually achieved by small-medium-sized mammals or birds (e.g., toucans) (SDD = 100-200m).

- Long: usually achieved by birds, bats or large-sized mammals such as primates (SDD > 200).

Jones LR, Duke-Sylvester SM, Leberg PL, Johnson DM (2017) Closing the gaps for animal seed dispersal: separating the effects of habitat loss on dispersal distances and seed aggregation. *Ecology and Evolution, 7*(14), 5410-5425

Seed survival, germination and establishment: Metrics measured in the primary studies categorized into "high" (major or adequate proportions of seeds arrived at the restored areas and survived/established), "medium" (moderate or acceptable proportions of seeds arrived into the restored areas and survived/established, according to the primary studies) and "low" (minor proportions of seeds arrived into the restored areas and survived/established).

Distance to reference forest: Presence/absence of undisturbed nearby reference forest which ensures connectivity and may act as a propagule source, specified in each primary study. As seed fall exponentially declines with increasing distance from the source (Hewitt & Kellman 2002; Ibáñez et al. 2014), it is assumed that the presence of undisturbed nearby forest would increase the amount of propagules, contributing to connectivity and that isolation reduces de amount of seed rain arriving in a fragment.

Seed Attack: Infestations, insects, fungi, seed harvesting. Categorized as a Yes/No response.

Climate: Presence/absence of the effect of climatic conditions such as high temperature and light intensity, which could promote seed desiccation, specified in each primary study.

Micro-environment: Biophysical influence of the area where seeds are deposited. Particularly, dispersed seeds will likely encounter new environmental conditions which influence seedling survival (O'Farrill et al., 2011). For instance, shade provided by the tree layer, soil conditions, presence/absence of other species that facilitate or compete for resources. Micro-environmental conditions of seed deposition were categorized as "improvement" (i.e., when the area where seeds were deposited favored seedling establishment and survival) or "competition" (i.e., when the area where seeds were deposited showed competitive conditions for seedling establishment).

O'Farrill G, Chapman CA & Gonzalez A (2011) Origin and deposition sites influence seed germination and seedling survival of Manilkara zapota: implications for long-distance, animal-mediated seed dispersal. *Seed Science Research, 21*(4), 305-313.

Perch effect: Presence/absence of perches or established trees which favor bird visits and seed depositions at specific sites.

Game: Hunting that affected animal seed dispersers populations.

Forest cover: Tree canopy cover reported in each primary study site and standardized into "continuous" (i.e., constant forest cover in the study area), "frequent" (i.e., large regenerating patches of forest in the study site) or "fragmented" (discontinuous and small forest fragments in the study site).

Restoration success: degree of restoration achieved according to the outcome reported by the authors in each publication for different characteristics, non-mutually exclusive: e.g., forest cover, plant and animal dispersers richness, seed survival and establishment: Ultimately, according to the degree of achievement in these characteristics, restoration success was categorized as "high", "medium", "low" or "unsuccessful" response.

- High: Achievement of continuous forest cover and/or high plant and animal dispersers richness and abundance, high seed survival and establishment.

(See for an example of this category of restoration success, Kelm et al. (2008) Effects of artificial roosts for frugivorous bats on seed dispersal in a Neotropical forest pasture mosaic. Conservation Biology, 22(3), 733-741.)

- Medium: Achievement of frequent forest cover, medium plant and animal dispersers richness and abundance, medium seed survival and establishment.

(See for an example of this category of restoration success, Herrera & García (2010) Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. Conservation biology, 24(4), 1089-1098.)

- Low: The system has been restored but some characteristics of the disturbed systems remain. E.g., fragmented forest cover, medium or low plant and animal dispersers richness and abundance, low seed survival establishment.

(See for an example of this category of restoration success Zhang & Chu (2015). Seed rain and seedling survival are major factors limiting vegetation regeneration on rehabilitated quarries. Landscape and ecological engineering, 11(1), 29-38.

- Unsuccessful: Most typical characteristics of disturbed systems still remain. E.g., fragmented forest cover, low plant and animal dispersers richness and abundance, low or no seed establishment.

(See for an example of this category of restoration success, Reid et al. (2013) Artificial bat roosts did not accelerate forest regeneration in abandoned pastures in southern Costa Rica. Biological Conservation, 167, 9-16.)

TABLE S1: Codes and descriptions for intrinsic and extrinsic dispersal factors.

Table S1. Codes and descriptions for intrinsic and extrinsic dispersal factors. For further details of variable categories in Supplement S2.

Code	Description
Extrinsic dispersal factors	
DISCAT	Disturbance category types which affected the study area and draw deforestation, defaunation and fragmentation. Mainly agriculture, alien spp., pastures and game (See Appendix 2A)
MANTYPE	Passive, assisted (active) or reconstructive (active) restoration approach.
MANAGE	Management age (i.e., time since land abandonment or management actions)
INITIAL	Initial conditions (highly degraded/least degraded)
PROTYPE	Forest protection type compiled to protected, unprotected and experimental site categories
FCOV	Type of forest cover summarized as continuous, frequent and fragmented
DISLIM	Distance limitations to reference habitat that acts as propagules (connectivity)
CLIMA	Climatic conditions (e.g., extreme events, seasonal shifts) limiting dispersal
MICRO	Micro-environment's biophysical influence in seed establishment (e.g., shade, soil conditions, presence/absence of nurse/competitive spp., compiled to improvement/competition)
GAME	Hunting that affects animal seed dispersers populations.
ATTACK	Seeds experience attack (i.e., seed dispersal and establishment are limited by infestations, light intensity, desiccation, seed predation and harvesting)
AGELIM	As a function of MANAGE, restoration is limited by the age of the system
Intrinsic dispersal factors	
BIRD	Bird species frugivory level (generalist or legitimate seed disperser)
MAM	Mammal species frugivory level (generalist or legitimate seed disperser)
ORD	Mammal species order category (e.g., rodentia, carnivora)
SIZE	Size of seeds dispersed (large > 10 mm; medium = 5-10 mm; small < 5 mm)
DISDIS	Animals' dispersal distance ability to introduce seeds into restored areas
HOAR	Hoarder behavior
PERCH	Presence of perches or stablished trees that favor animal dispersers visits
TROPH	Embedded trophic interactions among dispersers (i.e., pollination, predation, insectivory)
NDIS	Number of seeds dispersed into restoration area summarized as high, medium, low
NGER	Number of seeds germinated in the restoration area summarized as high, medium, low
NEST	Number of seeds established in the restoration area summarized as high, medium, low
aRich	Animal dispersers richness in the study area compiled as high, medium, low
aAbund	Animal dispersers abundance in the study area compiled as high, medium, low
pRich	Plant species richness in the study area compiled as high, medium, low
pAbund	Plant species abundance in the study area compiled as high, medium, low

SUPPLEMENT S3: Evolution of publications over time, disturbance categories, and most addressed intrinsic and extrinsic factors.

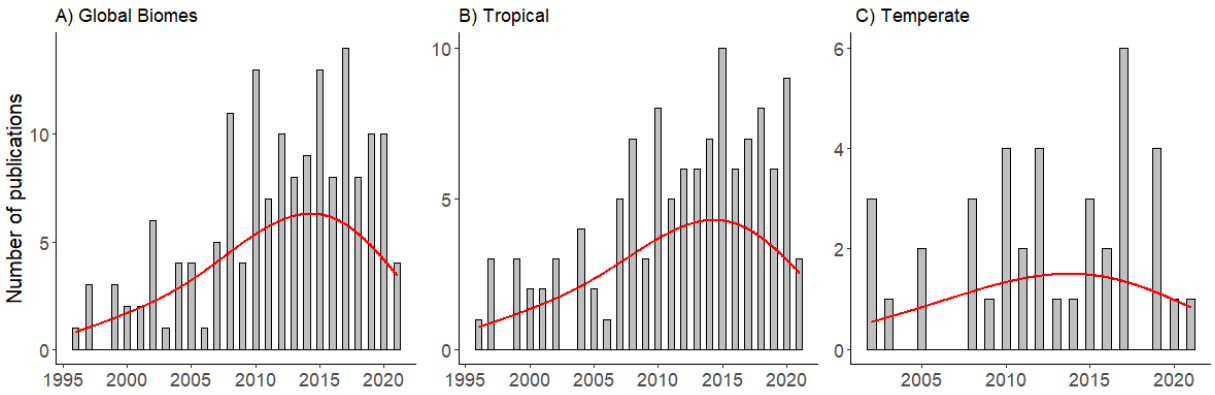


Figure S3.1. A) Global evolution of publications over time, regardless of biome type. B) Evolution of publications over time for Tropical systems. C) Evolution of publications over time for Temperate systems (note that publications in such systems begun in 2002). Red lines represent the Kernel density estimate.

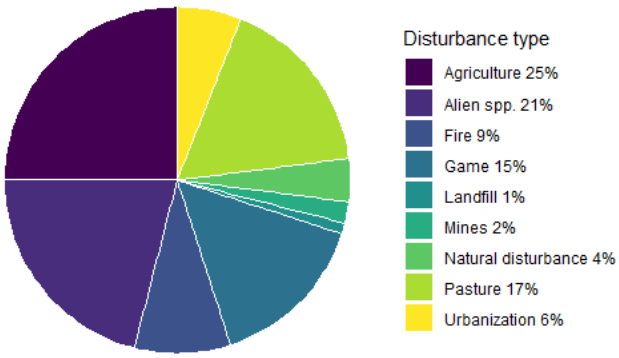


Figure S3.2. Percent distribution of disturbance category types according to the study sites.

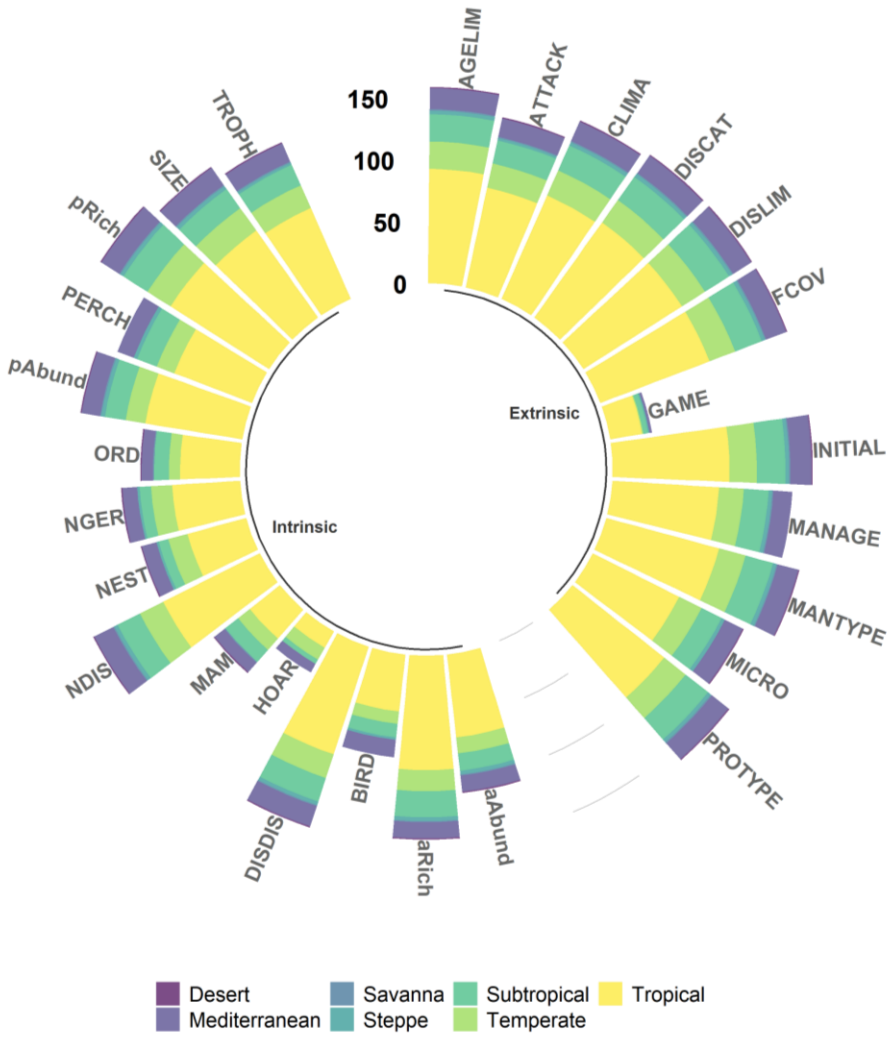


Figure S3.3. Intrinsic and extrinsic factors influencing restoration success addressed in the articles reviewed. For each factor the bar length indicates the number of studies that addressed it. Codes for (1) intrinsic factors: aAbund= disperser abundance, aRich= disperser richness, pRich=plant species richness, pAbund=plant abundance, BIRD=bird frugivory, DISDIS=dispersal distance ability, HOAR=hoarder activity, MAM=mammal frugivory, NDIS=number of seeds dispersed, NEST=number of seeds established, NGER=number of seeds germinated, ORD=mammal order, PERCH=perch effect, SIZE=seed size, TROPH=embedded trophic interactions, and (2) extrinsic factors: PROTYPE=forest protection type, MICRO=micro-environmental conditions, MANTYPE=management type, MANAGE=management age, INITIAL=initial conditions of the study site, GAME=game/hunting, FCOV=forest cover type, DISLIM=distance to reference habitat, DISCAT=disturbance category types, CLIMA=climatic effects, ATTACK=seed attack, AGELIM=restoration age.

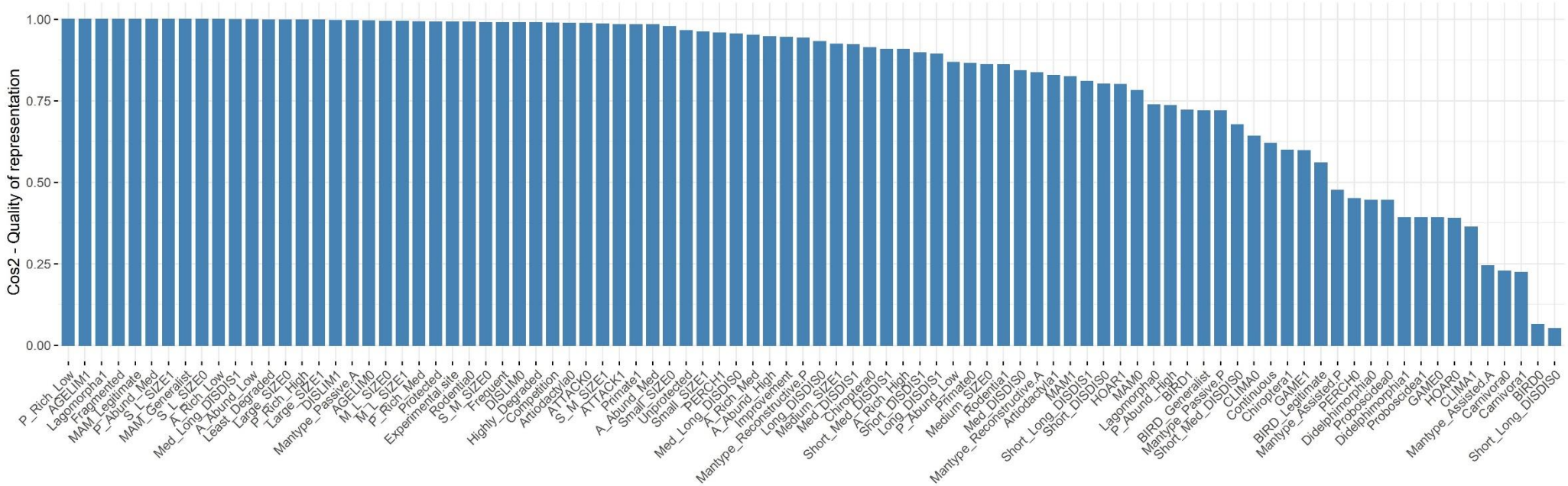
Table S2. Usage of intrinsic and extrinsic dispersal factors used to assess forest restoration for all publications, within each type of biome studied.

		Extrinsic dispersal factors											
Biome	**Total**	**PROTYPE**	**DISCAT**	**MAN AGE**	**MAN TYPE**	**AGELIM**	**DISLIM**	**ATTACK**	**MICRO**	**CLIMA**	**FCOV**	**GAME**	**INITIAL**
Tropical	94	94	94	86	94	92	94	82	78	91	94	26	94
Subtropical	23	23	23	20	23	22	23	19	18	22	23	4	23
Mediterranean	17	17	17	15	17	17	17	15	16	17	17	2	17
Temperate	22	22	22	20	22	22	22	20	20	22	22	1	22
Desert	1	1	1	0	1	1	1	1	1	1	1	0	1
Steppe	3	3	3	3	3	3	3	2	3	3	3	1	3
Savanna	1	1	1	1	1	1	1	1	0	1	1	0	1
Total publications	161	161	161	145	161	158	161	140	136	157	161	34	161

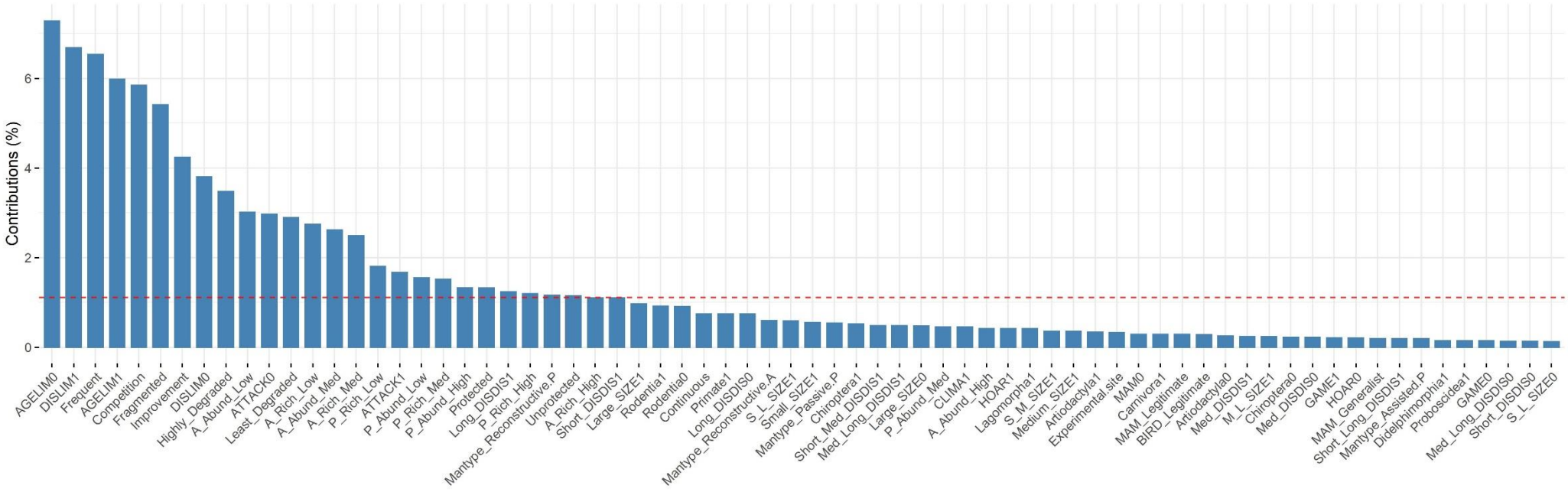
		Intrinsic dispersal factors														
	Total	**BIRD**	**MAM**	**ORD**	**SIZE**	**HOAR**	**TROPH**	**DISDIS**	**PERCH**	**NDIS**	**NGER**	**NEST**	**aAbund**	**pAbund**	**aRich**	**pRich**
Tropical	94	46	31	48	86	15	80	91	67	87	55	49	92	94	92	94
Subtropical	23	11	13	12	19	4	18	20	17	20	9	8	21	23	21	23
Mediterranean	17	14	10	9	17	8	16	17	14	17	12	12	17	17	17	17
Temperate	22	10	12	9	22	11	20	20	15	21	17	16	22	22	22	22
Desert	1	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1
Steppe	3	2	0	0	3	0	2	3	3	3	2	2	3	3	3	3
Savanna	1	0	1	1	1	0	1	1	0	1	0	0	1	1	1	1
Total publications	161	83	68	80	149	38	137	153	116	98	96	88	157	161	157	161

SUPPLEMENT S4: Quality of representation tests and variable contributions of the Correspondence Analysis.

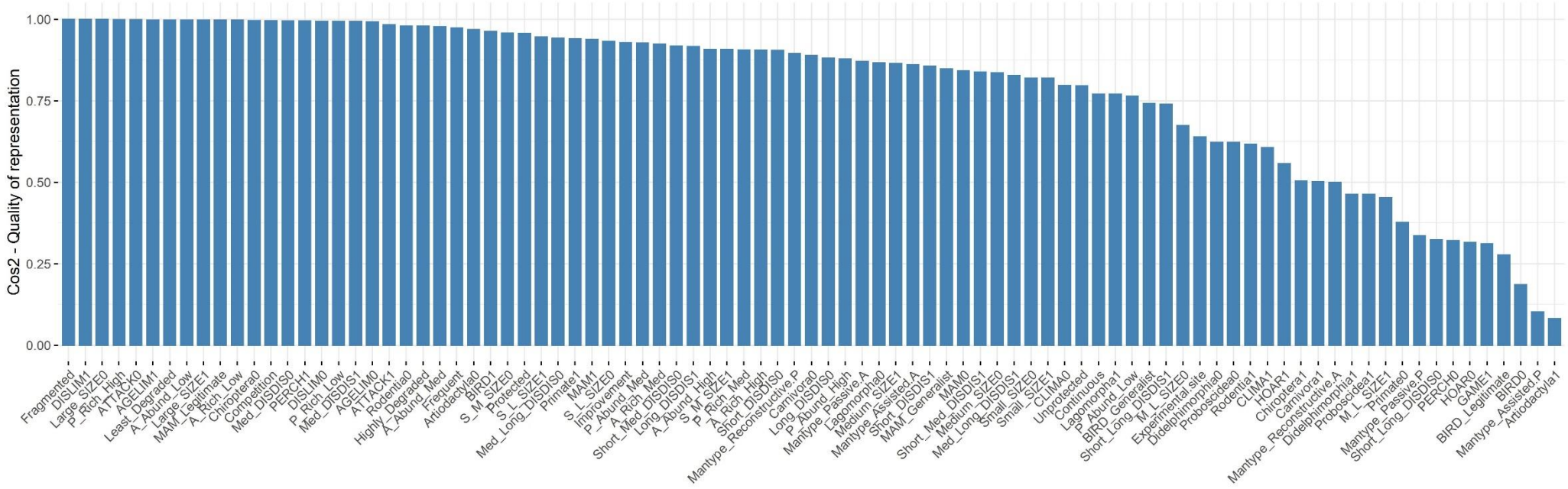
A) The Cos2 quality of representation for global biomes (measured by the square cosine, Cos2). Measure of the degree of association between the variables and a particular axis (i.e., how good the representation of the variables on each component is).



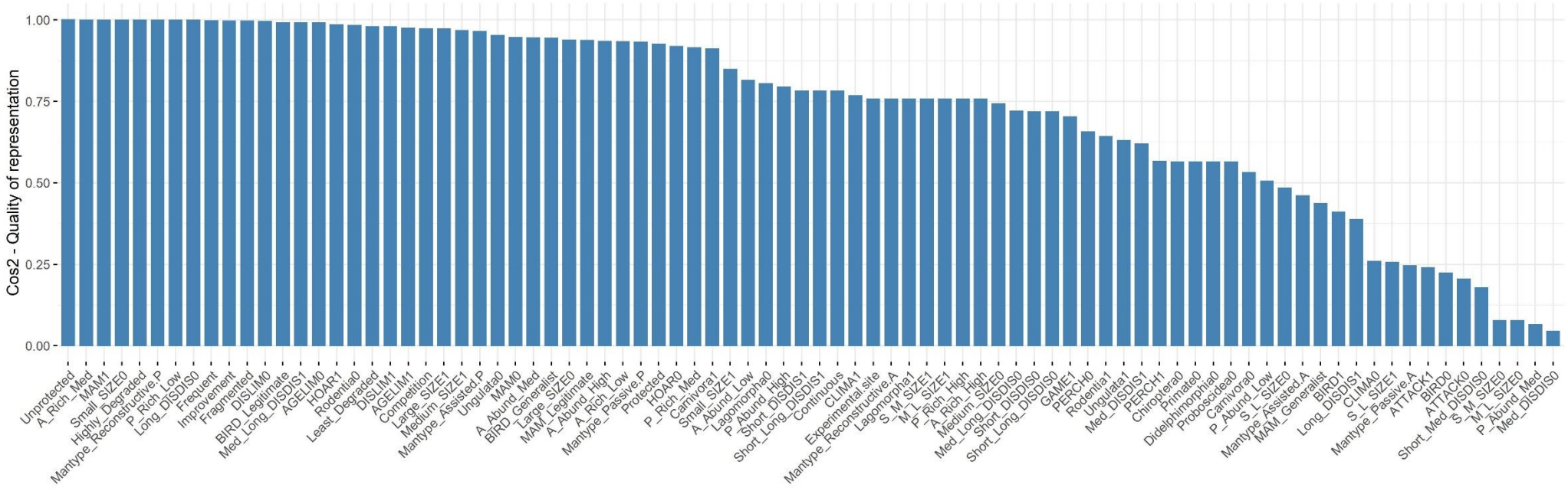
B) Contribution of variables for global biomes. Red-dashed line corresponds to the reference expected value if the contribution of all variables were uniform. Any variable with a contribution above the reference line is considered to importantly contribute to the dimension.



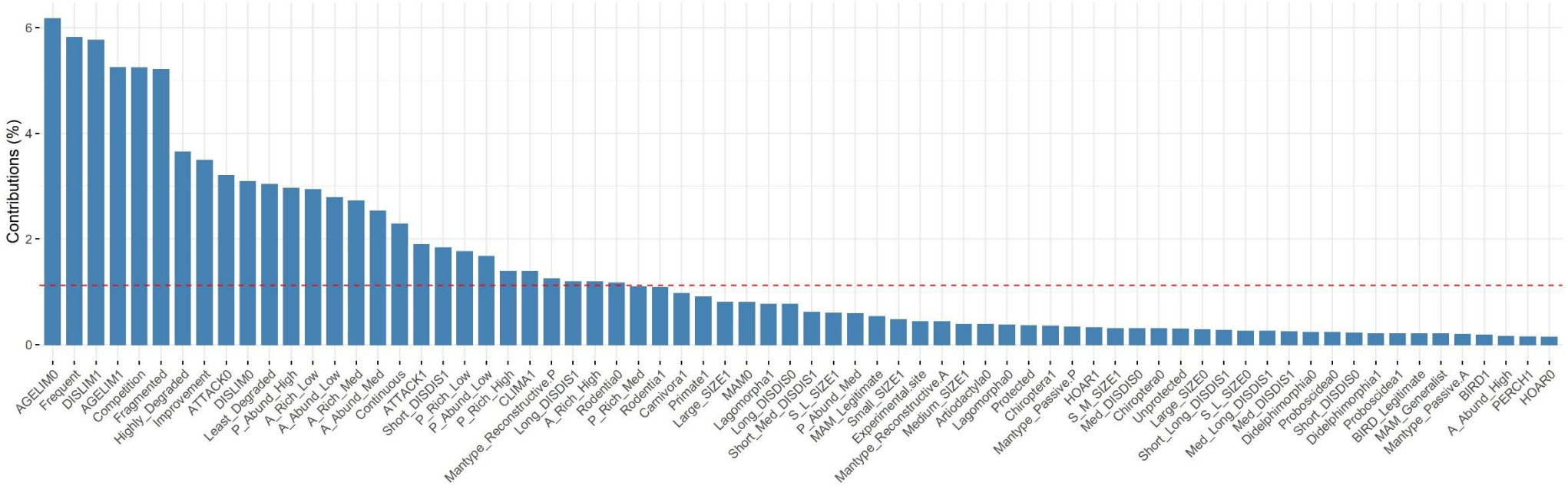
C) The Cos2 quality of representation for Tropical biomes (measured by the square cosine, Cos2). Measure of the degree of association between the variables and a particular axis (i.e., how good the representation of the variables on each component is).



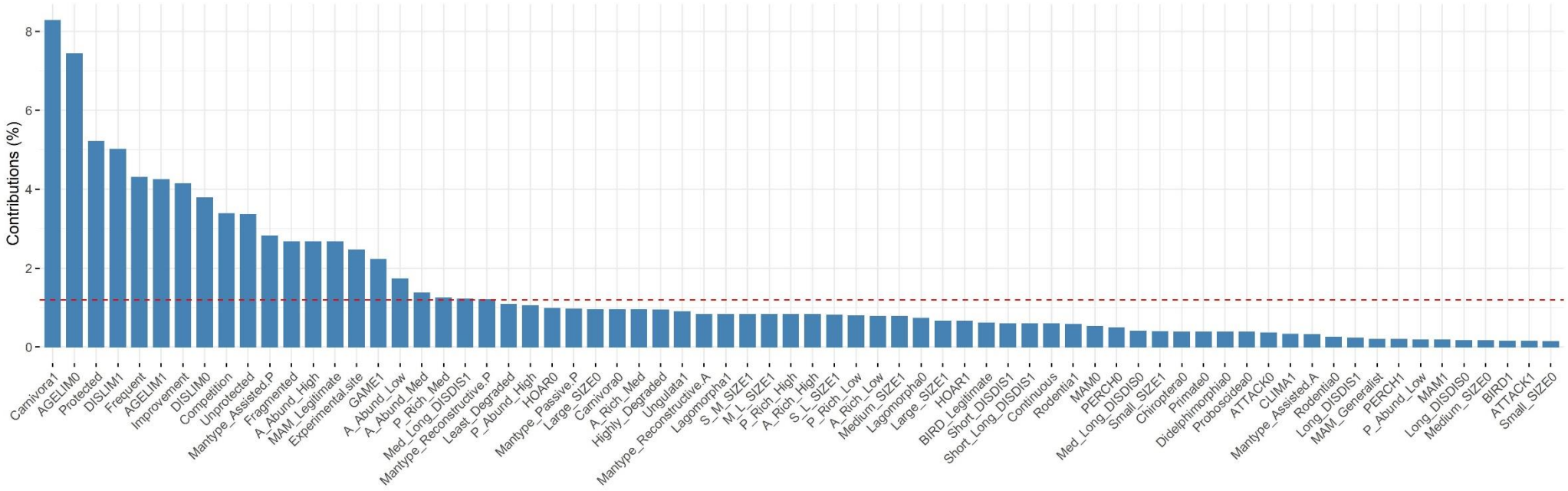
D) The Cos2 quality of representation for Temperate biomes (measured by the square cosine, Cos2). Measure of the degree of association between the variables and a particular axis (i.e., how good the representation of the variables on each component is).



E) Contribution of variables for Tropical biomes. Red-dashed line corresponds to the reference expected value if the contribution of all variables were uniform. Any variable with a contribution above the reference line is considered to importantly contribute to the dimension.

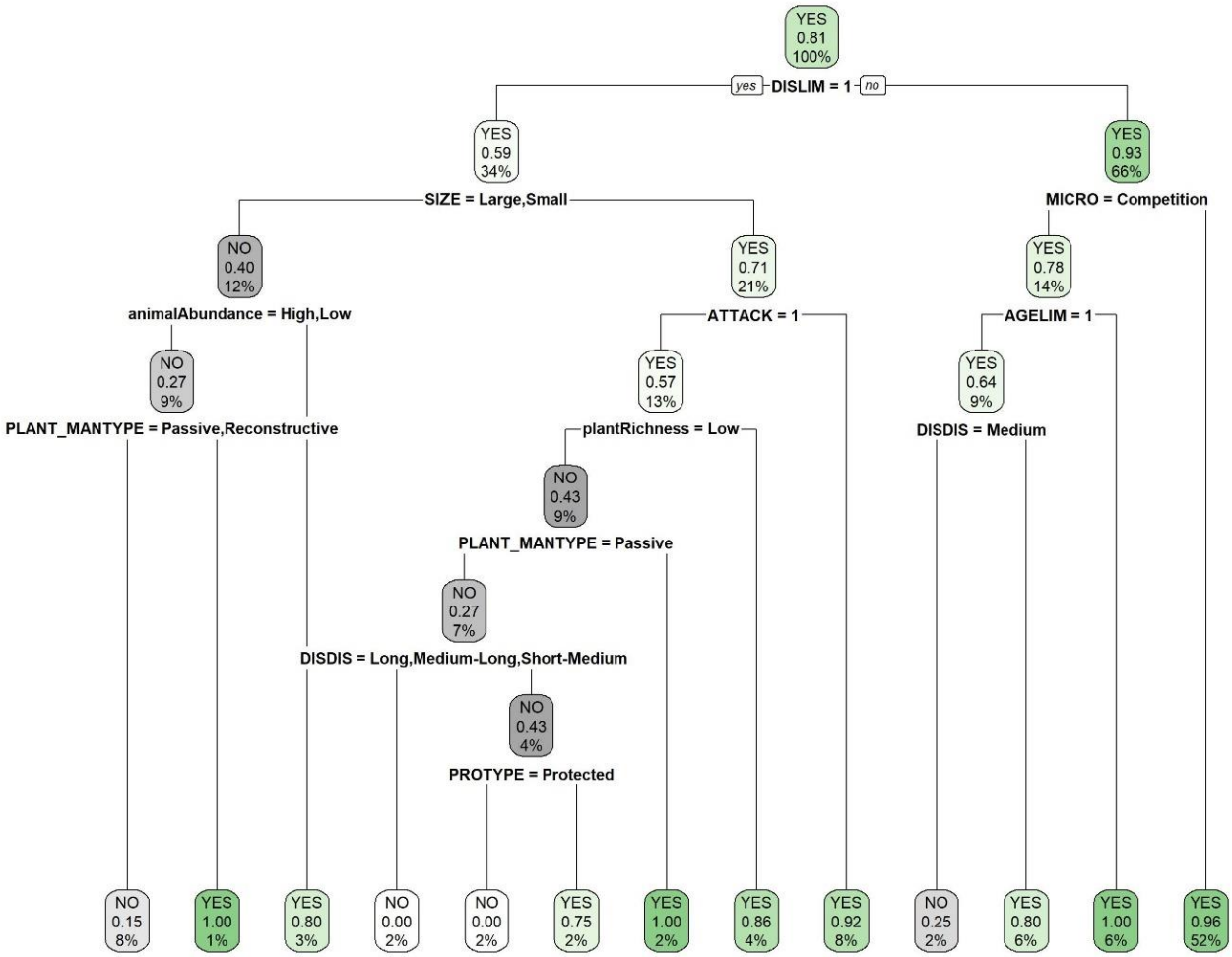


F) Contribution of variables for Temperate biomes. Red-dashed line corresponds to the reference expected value if the contribution of all variables were uniform. Any variable with a contribution above the reference line is considered to importantly contribute to the dimension.



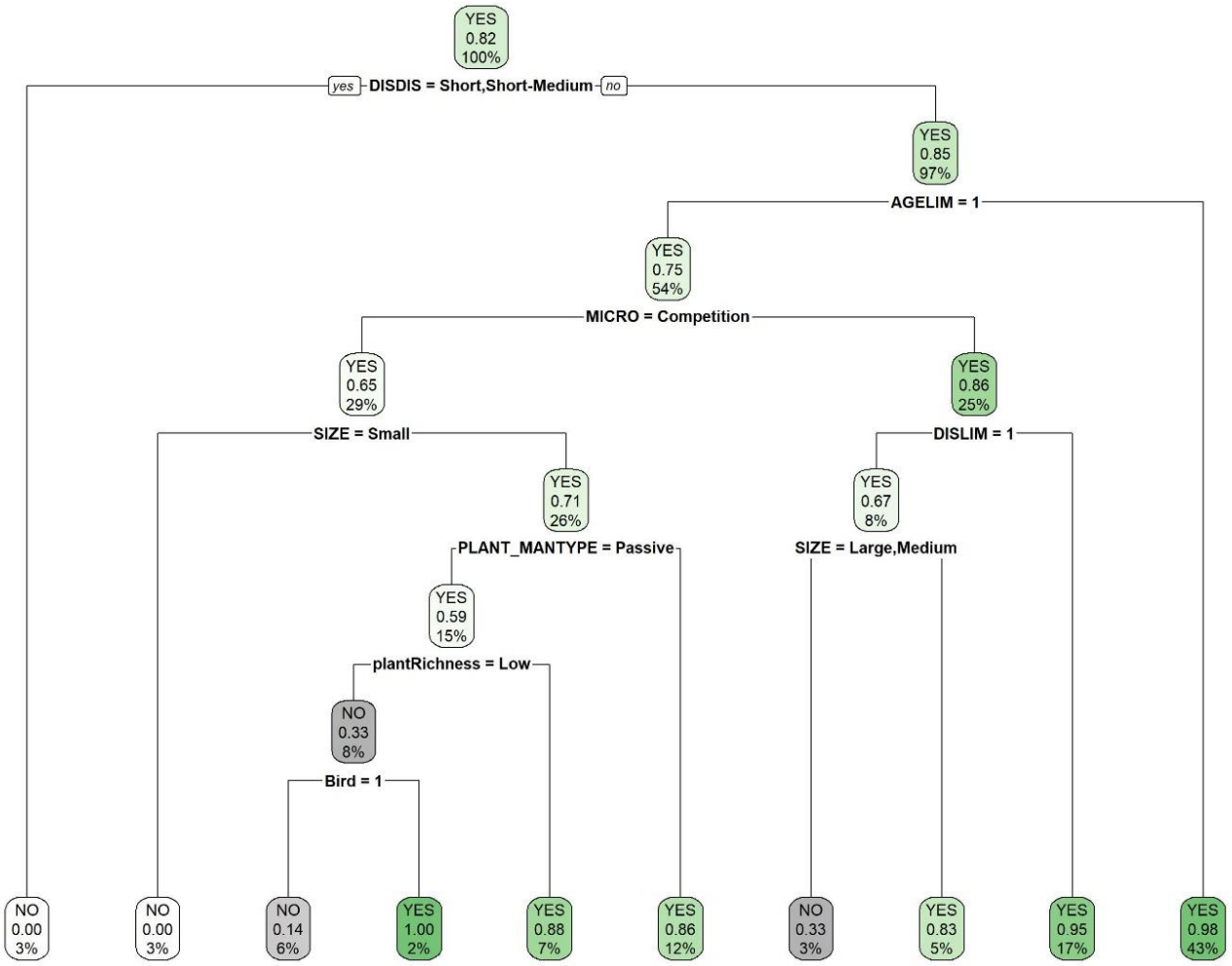
SUPPLEMENT S5: Classification Tree Analysis layout.

A) Classification Tree Analysis outcome for global biomes. (See Supplement S3 for variable codes and descriptions). Notice that the decision outcome of the end nodes does not sum up to 100% due to automatic decimal rounding.



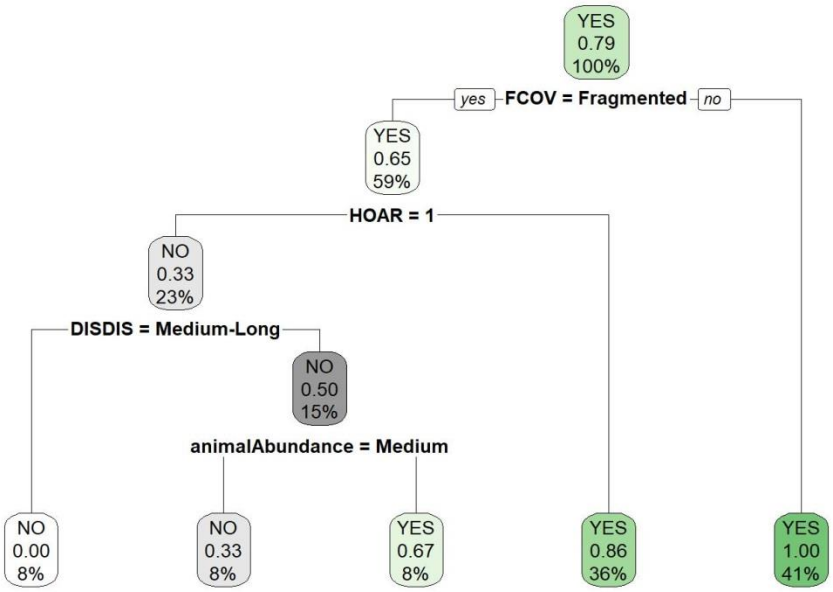
B)

Classification Tree Analysis outcome for Tropical biomes. (See Supplement S3 for variable codes and descriptions). Notice that the decision outcome of the end nodes does not sum up to 100% due to automatic decimal rounding.



C)

Classification Tree Analysis outcome for Temperate biomes. (See Supplement S3 for variable codes and descriptions). Notice that the decision outcome of the end nodes does not sum up to 100% due to automatic decimal rounding.



Appendix 2

Supplementary material – Chapter 3

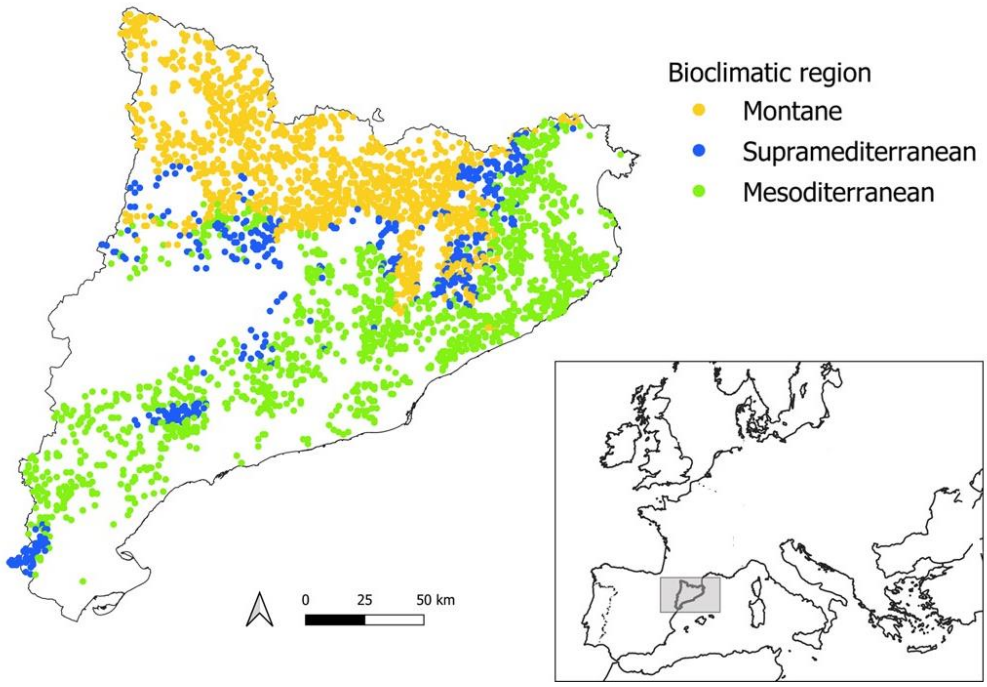


Figure S1: Study area and geographical distribution of the National Forest Inventory plots considered in our study of Catalonia (NE Spain). The Spanish National Forest Inventory plots are permanent plots located in a 1 × 1 km grid covering all forested areas of Spain. Although the first inventory was conducted in the 1960´s (NFI1), it was not until the second inventory (NFI2) that it was designed as a systematic and continuous sample of concentric circular plots. For each inventory, each survey plot consisted of four concentric subplots with 5-m radius, 10-m radius, 15-m radius, and 25-m radius (to measure trees with 7.5, 12.5, 22.5 and more than 42.5 cm of diameter at breast height [dbh], respectively). In addition, in the 5-m radius plot, trees with dbh 2.5–7.5 cm were also identified (Alberdi et al., 2016). Data corresponds to the second (NFI2) and fourth (NFI4) Spanish National Forest Inventories, which in Catalonia took place during 1989-1990 and 2013-2016. As the NFI4 only covered a sub-sample of the plots previously inventoried in the NFI2, for the purposes of this study we selected those plots that were sampled in both inventories (N=3397). From this dataset, we excluded forests affected by wildfires during the studied period (1989-2016; 256 plots; 7.83%) given that the post-fire regeneration process and the influencing factors have been widely studied elsewhere (see among others Rodrigo et al. 2004). Burned plots

from 1989 to 2016 were identified and discarded using wildfire maps provided by the Generalitat de Catalunya (https://interior.gencat.cat/es/arees_dactuacio/bombers/foc-forestal/incendis_forestals/). This selection resulted in a final number of 3141 plots retained and showed in the map. Fill colours represent the Bioclimatic region for each plot, defined by the thermicity index (orange = montane, blue = supramediterranean and green = mesomediterranean).

Table S1: List of tree species (N = 71) present in the national forest inventory (NFI) dataset for Catalonia. Names in bold show the most representative tree species due to their presence in more than five plots (N=50). Asterisks (*) represent those tree species that were only recorded by genus in the NFI2 and were later identified by species by reason of the NFI4 replicated plots. Squares (▪) represent those tree species for which the genus was maintained due to inconsistencies in their identification among both NFIs.

Species ID	
Abies alba	***Pinus halepensis***
Acer campestre*	***Pinus nigra***
Acer monspessulanum*	***Pinus pinaster***
Acer negundo	***Pinus pinea***
Acer opalus*	***Pinus radiata***
Acer platanoides	***Pinus sylvestris***
Acer pseudoplatanus*	***Pinus uncinata***
Alnus glutinosa	***Platanus hispanica****
Arbutus unedo	***Populus alba***
Betula spp. ▪	***Populus nigra***
Castanea sativa	***Populus tremula***
Cedrus atlantica	***Populus x canadensis***
Cedrus libani	***Prunus spp.*** ▪
Celtis australis	***Prunus avium***
Ceratonia siliqua	***Pseudotsuga menziesii***

Corylus avellana	*Pyrus spp.*
Crataegus monogyna*	***Quercus canariensis***
Cupressus arizonica	***Quercus faginea***
Cupressus sempervirens	***Quercus pubescens****
Eucalyptus camaldulensis	***Quercus ilex***
Fagus sylvatica	***Quercus petraea***
Ficus carica	***Quercus pyrenaica****
Fraxinus angustifolia*	***Quercus robur****
Fraxinus excelsior*	*Quercus rubra*
Ilex aquifolium	***Quercus suber***
Juglans regia	*Rhamnus alaternus*
Juniperus communis*	***Robinia pseudacacia***
Juniperus oxycedrus*	***Salix spp.*** ▪
Juniperus phoenicea	***Sambucus nigra***
Juniperus thurifera	***Sorbus spp.*** ▪
Larix decidua	*Taxus baccata*
Laurus nobilis	***Tilia spp.*** ▪
Malus sylvestris	*Ulmus glabra*
Olea europaea	***Ulmus minor****
Phillyrea latifolia	*Ulmus pumila*
Picea abies	

Table S2: Tree species functional trait data regarding seed dispersal type, shade tolerance and drought tolerance, together with each species cluster classification according to the three studied functional traits using the Gower distance and the Ward algorithm (Kassambara, 2017). Data for dispersal type, shade tolerance and drought tolerance was extracted from the TRY (Kattge et al., 2011), BROT 2.0 (Tavşanoğlu & Pausas, 2018) and Niinemets & Valladares, 2006 databases. For those species for which there was more than one measurement for the same shade or drought tolerance metric, we computed the mean value, while for those species with no information available on the abovementioned databases or that were only identified at the genus level in the forest inventories, we computed the mean trait value across other species for the same genus (see

García-Valdés et al., 2021 for a similar procedure). The animal dispersed group included vertebrate dispersed species while the other methods group included anemochorous, myrmechorous and barochorous species. Species for which data was not available were removed from the analysis explaining the role of functional traits for recruitment, resulting in a total number of 43 species used. Cluster classifications correspond to: Cluster 1 = animal dispersed species with relatively lower drought tolerance and higher shade tolerance; Cluster 2 = animal dispersed species with relatively higher drought tolerance and lower shade tolerance; Cluster 3 = species with other dispersal methods with relatively lower drought tolerance and higher shade tolerance; and Cluster 4 = species with other dispersal methods and relatively higher drought tolerance and lower shade tolerance.

Species ID	Dispersal type	Shade Tolerance	Drought Tolerance	Cluster Classification
Abies alba	Other methods	4.6	1.81	3
Acer campestre	Other methods	3.18	2.93	3
Acer monspessulanum	Other methods	2.66	4.31	4
Acer opalus	Other methods	3.48	3.72	3
Acer pseudoplatanus	Other methods	NA	NA	NA
Alnus glutinosa	Animal	2.71	2.22	1
Arbutus unedo	Animal	2.66	3.9	2
Betula spp.	Other methods	2.03	1.85	3
Castanea sativa	Animal	3.15	3.46	2
Corylus avellana	Animal	3.53	3.04	1
Crataegus monogyna	Animal	1.93	3.46	2
Fagus sylvatica	Animal	4.56	2.4	1

Fraxinus angustifolia	Other methods	2.73	2.59	3
Fraxinus excelsior	Other methods	2.66	2.5	3
Ilex aquifolium	Animal	3.86	3.04	1
Juglans regia	Animal	NA	NA	NA
Juniperus communis	Animal	NA	NA	NA
Juniperus oxycedrus	Animal	NA	NA	NA
Juniperus phoenicea	Animal	NA	NA	NA
Olea europaea	Animal	1.53	4.64	2
Phillyrea latifolia	Animal	2.78	4.64	2
Pinus halepensis	Other methods	1.35	4.97	4
Pinus nigra	Other methods	2.1	4.38	4
Pinus pinaster	Animal	1.8	3.71	2
Pinus pinea	Animal	1.8	3.71	2
Pinus radiata	Other methods	2.97	3	3
Pinus sylvestris	Other methods	1.67	4.34	4
Pinus uncinata	Other methods	1.2	3.88	4
Platanus hispanica	Other methods	2.95	3.03	3
Populus alba	Other methods	2.3	2.67	3
Populus nigra	Other methods	2.46	2.2	3
Populus tremula	Other methods	2.22	2.85	3
Populus x canadensis	Other methods	1.67	1.77	3
Prunus spp.	Animal	2.54	2.06	1

Prunus avium	Animal	3.33	2.66	1
Pseudotsuga menziesii	Other methods	2.78	2.62	3
Quercus canariensis	Animal	2.52	3.76	2
Quercus faginea	Animal	2.52	3.76	2
Quercus ilex	Animal	3.02	4.72	2
Quercus petraea	Animal	2.73	3.02	1
Quercus pubescens	Animal	2.52	3.76	2
Quercus pyrenaica	Animal	2.52	3.76	2
Quercus robur	Animal	2.45	2.95	1
Quercus suber	Animal	2.52	3.76	2
Robinia pseudacacia	Other methods	1.72	4.11	4
Salix spp.	Other methods	1.61	1.63	3
Sambucus nigra	Animal	NA	NA	NA
Sorbus spp.	Animal	3	3.55	2
Tilia spp.	Other methods	NA	NA	NA
Ulmus minor	Other methods	3.36	3.39	3

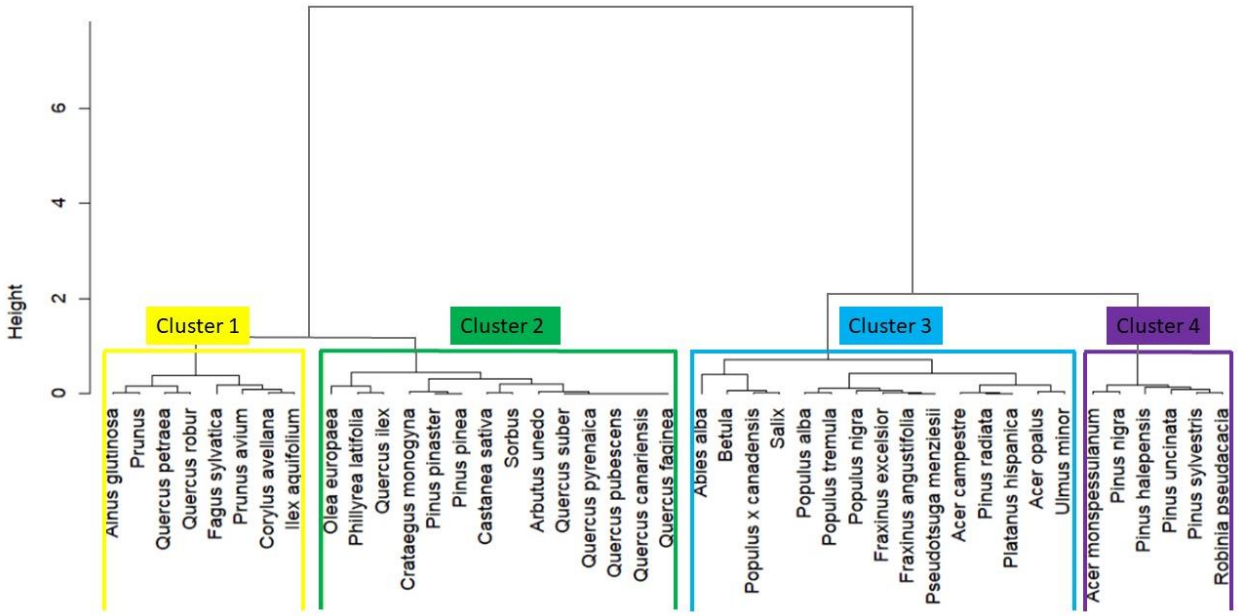


Figure S2: Dendrogram of the hierarchical cluster classification for each tree species in relation to their dispersal method, shade tolerance and drought tolerance functional trait data. Cluster classifications correspond to: Cluster 1 = animal dispersed species with relatively lower drought tolerance and higher shade tolerance; Cluster 2 = animal dispersed species with relatively higher drought tolerance and lower shade tolerance; Cluster 3 = species with other dispersal methods with relatively lower drought tolerance and higher shade tolerance; and Cluster 4 = species with other dispersal methods and relatively higher drought tolerance and lower shade tolerance.

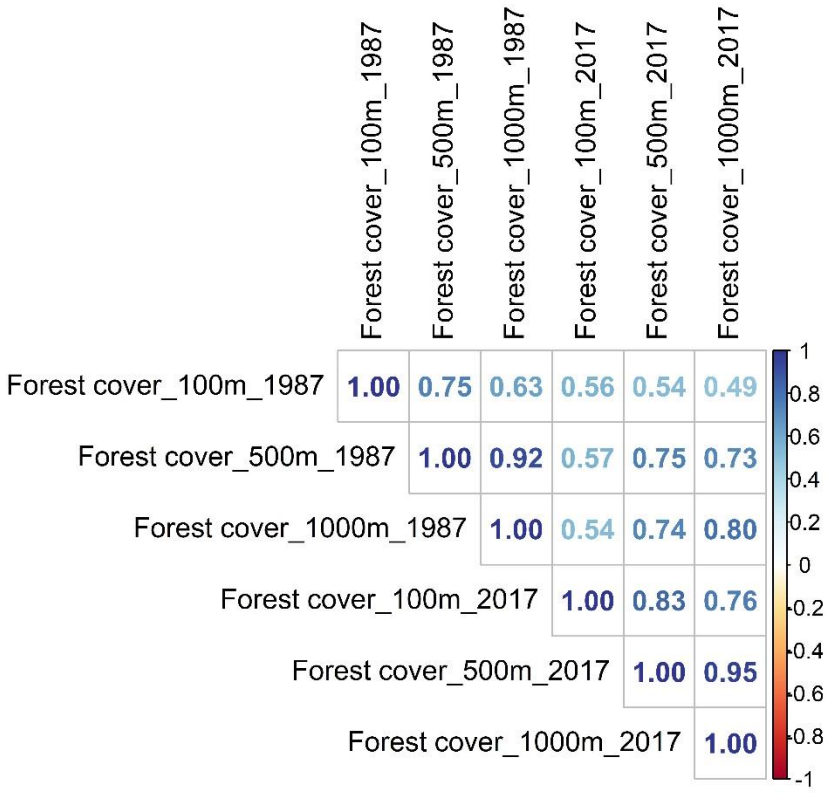
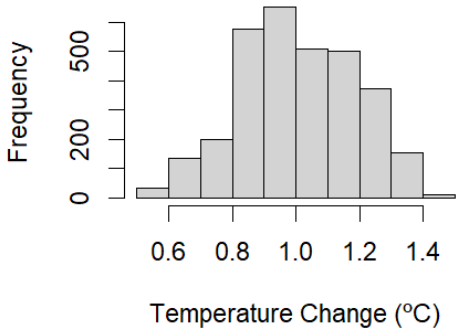


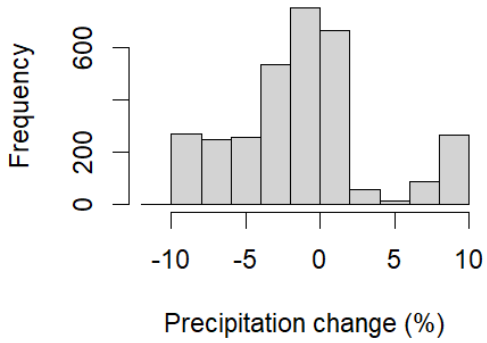
Figure S3: Pearson correlation matrix for the proportion of forest cover (%) surrounding the NFI plots at 100m, 500m and 1000m radius derived from land cover maps of Catalonia for the years 1987 and 2017. The proportion of forest cover was considered to account for forest connectivity in the landscape.

(A)



Min.	0.55
1st Qu.	0.86
Median	0.99
Mean ± std error	1.00 ± 0.003
3rd Qu.	1.15
Max.	1.47

(B)



Min.	-11.54
1st Qu.	-3.98
Median	-0.96
Mean ± std error	-1.22 ± 0.09
3rd Qu.	1.09
Max.	9.51

Figure S4: Trends and summaries of temperature (A) and precipitation (B) changes during 1988–1992 (as representative of the NFI2 period), and the years 2011–2015 (as representative of the NFI4 period) obtained from the Climate Engine database (https://www.climateengine.org/) at 9.6 km daily resolution (AgERA5) for the study site. The histograms represent the frequency distribution of the values for temperature and precipitation changes for all the National Forest Inventory plots for Catalonia, while the tables show a summary of the minimum (Min.), first quantile (1st Qu.), median, mean and standard error of the mean (Mean ± std error), third quantile (3rd Qu.) and maximum (Max.) values for each distribution.

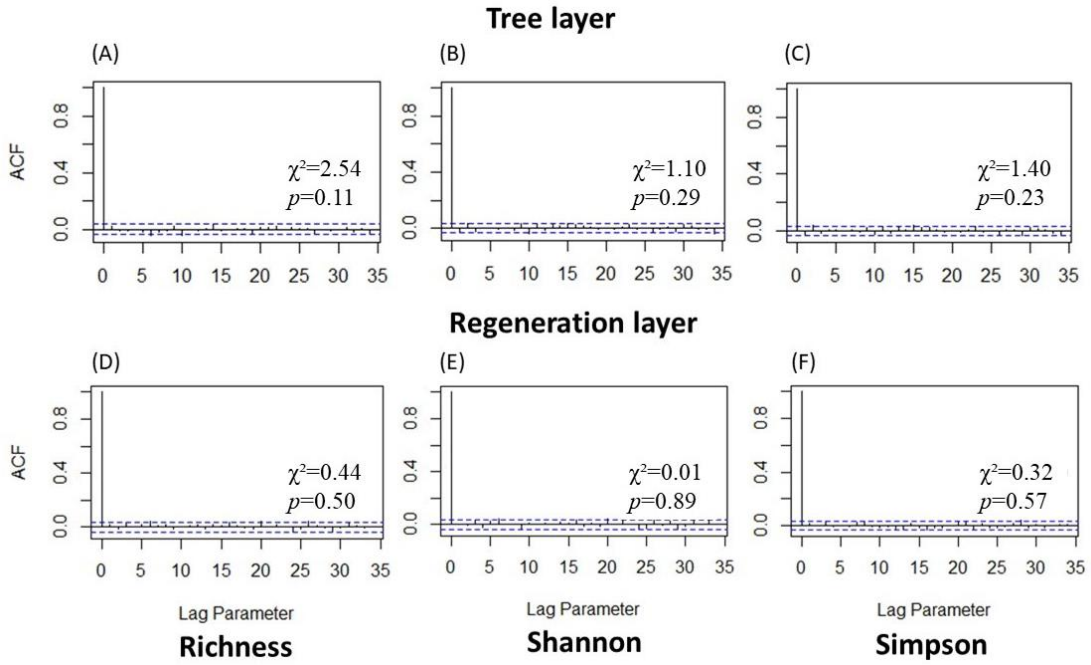


Figure S5: Results of the residual's spatial autocorrelation test for the linear mixed effect models explaining species richness change, Shannon diversity index change and Simpson diversity index change for the tree and regeneration layers. Explanatory variables included management and environmental factors. Spatial autocorrelation of the residuals was tested using Ljung-Box tests and the ACF autocorrelation function (Stats *package* (R Core Team, 2018)). The values of the chi-squared and respective p values are shown indicating absence of spatial autocorrelation ($p>0.05$ for all cases). Figures A, B and C correspond to the tree layer while Figures D, E, F correspond to the regeneration layer.

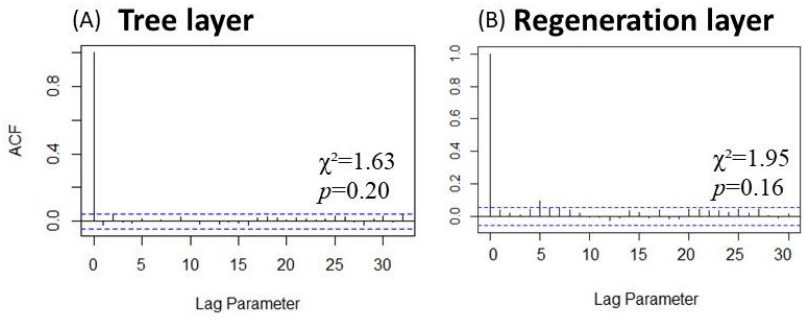


Figure S6. Results of the residual's spatial autocorrelation test for the generalized linear mixed effect models explaining recruitment likelihood from inside (i.e., 1) or outside (i.e., 0) the plots for the tree (A) and regeneration (B) layers. Explanatory variables included management and environmental factors, together with species functional trait characteristics. Spatial autocorrelation of the residuals was tested using Ljung-Box tests and the ACF autocorrelation function (Stats *package* (R Core Team, 2018)). The values of the chi-squared and respective p values are shown indicating absence of spatial autocorrelation (p>0.05 for all cases).

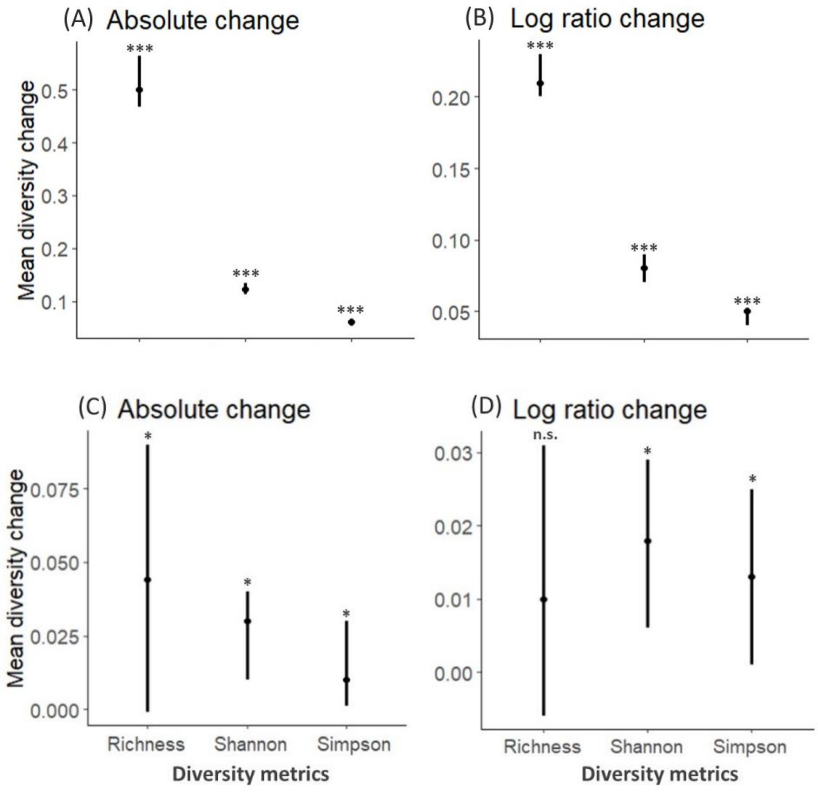


Figure S7: Tree and regeneration layer's sensitivity tests of log ratio changes for species richness (Hill number q=0), Shannon diversity index (Hill number q=1) and Simpson diversity index (Hill number q=2). Figures A and B show the absolute change and the log ratio change, respectively for the tree layer. Figures C and D show the absolute and the log ratio change, respectively for the regeneration layer. Notice that for the tree layer the absolute change and the log ratio change follow the same pattern and significance, however, for the regeneration layer, although the Shannon diversity index and the Simpson diversity index show the same pattern and significance, the species richness log ratio change was not significant. Log ration changes were not computed for the Pielou's Evenness index, as the change from the NFI2 to the NFI4 was not significant.

Table S3. Permutation test results for the tree and regeneration layers' tree species abundance and presence/absence computed using the anosim function (*vegan* package, Oksanen et al., 2007). Anosim statistic R values closer to 1 show high dissimilarities between inventories and in view of the p-value, differences are significant (p=0.001).

	Abundance		Presence/Absence	
	Anosim statistic R	*Significance p*	*Anosim statistic R*	*Significance p*
Tree layer	0.80	0.001	0.80	0.001
Regeneration	0.71	0.001	0.72	0.001

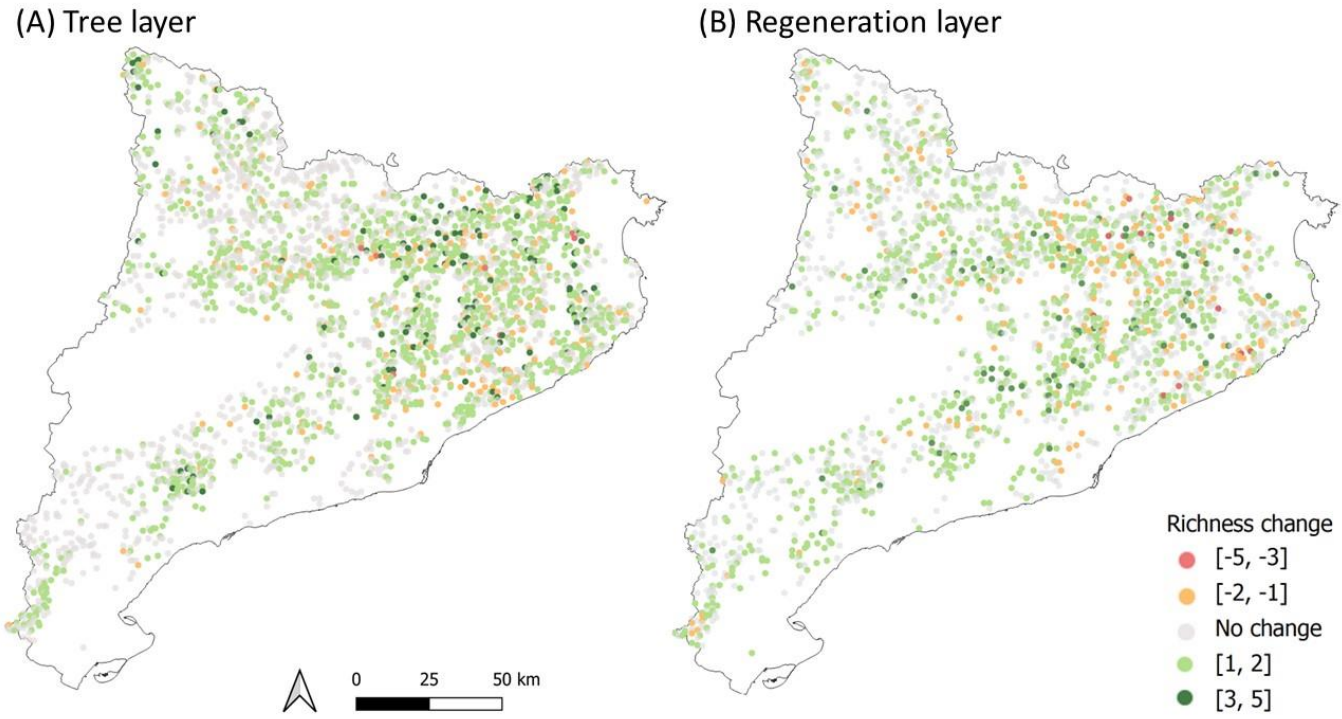


Figure S8. Spatial distribution of species richness changes for the plots of the Spanish National Inventory in the study area during the study period (1989-2016) for (A) the tree layer, and (B) the regeneration layer. In total, 39% of the plots gained species for the tree layer, while 30% of the plots for the regeneration layer. Coloured points represent the range in the number of species lost

or gained: in red those plots that lost from 5 to 3 species; in orange those plots that lost from 2 to 1 species; in grey those plots in which the number of species did not change during the study period; in light green those plots that gained from 1 to 2 species; and in dark green those plots that gained from 3 to 5 species.

Table S4: Results of the linear model for species richness change from the NFI2 (1989) to the NFI4 (2016) for the tree layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, and temperature and precipitation changes) best predicted the response (i.e., richness change), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). The resulting explicative variables explaining species richness change included the bioclimatic region, land use history, forest cover, protection, past management, recent management, basal area (m^2/ha), and temperature and precipitation changes. P values indicating the significant effects are highlighted in bold. The number of plots (NFI plots), R^2 and R^2 adjusted values, and the models' AIC value are also shown.

	Tree layer species Richness change		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.34	0.22 – 0.45	**<0.001**
Montane	0.32	0.16 – 0.47	**<0.001**
Supramediterranean	0.24	0.03 – 0.45	**0.026**
Long-established forest	0.20	0.08 – 0.32	**0.001**
Forest cover	-0.04	-0.12 – 0.04	0.362

Protection	-0.06	-0.13 – 0.01	0.116
Past management	0.08	-0.02 – 0.19	0.08
Recent management	-0.37	-0.51 – -0.23	**<0.001**
Basal area	-0.16	-0.22 – -0.11	**<0.001**
Temperature change	-0.14	-0.20 – -0.09	**<0.001**
Precipitation change	-0.15	-0.20 – -0.09	**<0.001**
NFI plots	3141		
R^2 / R^2 adjusted	7.3% / 6.6%		
Lowest AIC	8554.29		

Table S5: Results of the linear model for the Shannon diversity index change from the NFI2 (1989) to the NFI4 (2016) for the tree layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, and temperature and precipitation changes) best predicted the response (i.e., Shannon diversity change), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). The resulting explicative variables explaining species richness change included the bioclimatic region, land use history, forest cover, protection, past management, recent management, basal area (m^2/ha), and temperature and precipitation change. P values indicating the significant effects are highlighted in bold. The number of plots (NFI plots), R^2 and R^2 adjusted values, and the models' AIC value are also shown.

	Tree layer Shannon diversity index change		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.08	0.04 – 0.11	**<0.001**
Montane	0.06	0.02 – 0.11	**0.009**
Supramediterranean	0.08	0.01 – 0.14	**0.019**
Long-established forest	0.07	0.03 – 0.11	**<0.001**
Forest cover	-0.00	-0.01 – 0.01	0.970
Protection	-0.02	-0.04 – 0.01	0.184
Past management	0.02	-0.01 – 0.05	0.261
Recent management	-0.07	-0.11 – -0.03	**<0.001**
Basal area	-0.06	-0.09 – -0.03	**<0.001**
Temperature change	-0.04	-0.06 – -0.03	**<0.001**
Precipitation change	-0.02	-0.04 – -0.01	**<0.001**
Observations	3141		
R^2 / R^2 adjusted	5.1% / 4.5%		
Lowest AIC	1112.03		

Table S6: Results of the linear model for the Simpson diversity index change from the NFI2 (1989) to the NFI4 (2016) for the tree layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, and temperature and precipitation changes) best predicted the response (i.e., Simpson diversity change), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). The resulting explicative variables explaining species richness change included the bioclimatic region, land use history, forest cover, protection, past management, recent management, basal area (m^2/ha), and temperature and precipitation changes. P values indicating the significant effects are highlighted in bold. The number of plots (NFI plots), R^2 and R^2 adjusted values, and the models' AIC value are also shown.

	Tree layer Simpson diversity index change		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.04	0.02 – 0.06	**<0.001**
Montane	0.02	-0.01 – 0.05	0.200
Supramediterranean	0.05	0.01 – 0.08	**0.017**
Long-established forest	0.03	0.01 – 0.06	**0.003**
Forest cover	-0.00	-0.01 – 0.01	0.723
Protection	-0.01	-0.02 – 0.01	0.405
Past management	0.01	-0.01 – 0.03	0.389

Recent management	-0.04	-0.06 – -0.01	**0.002**
Basal area	-0.02	-0.04 – -0.01	**<0.001**
Temperature change	-0.02	-0.03 – -0.01	**<0.001**
Precipitation change	-0.00	-0.02 – 0.01	0.653
Observations	3141		
R^2 / R^2 adjusted	3.8% / 3.3%		
Lowest AIC	2293.15		

Table S7: Results of the linear model for species richness change from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area and temperature and precipitation changes) best predicted the response (i.e., richness change), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). The resulting explicative variables explaining species richness change included the bioclimatic region, land use history, forest cover, protection, past management, recent management, basal area (m^2/ha), and temperature and precipitation changes. P values indicating the significant effects are highlighted in bold. The number of plots (NFI plots), R^2 and R^2 adjusted values, and the models' AIC value are also shown.

	Regeneration layer Species Richness change		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.09	-0.21 – 0.14	**0.017**
Montane	-0.06	-0.20 – 0.09	0.312
Supramediterranean	-0.06	-0.20 – 0.09	0.444
Long-established forest	0.21	0.07 – 0.34	**0.002**
Forest cover	-0.04	-0.10 – 0.01	0.142
Protection	0.18	0.01 – 0.36	**0.042**
Past management	-0.13	-0.26 – 0.00	0.056
Recent management	-0.31	-0.56 – -0.06	**0.016**
Basal area	-0.41	-0.53 – -0.29	**<0.001**
Temperature change	0.10	0.03 – 0.11	**0.008**
Precipitation change	0.17	0.09 – 0.23	**<0.001**
Observations	3141		
R^2 / R^2 adjusted	6.5% / 5.7%		
Lowest AIC	10000.7		

Table S8: Results of the linear model for the Shannon diversity index change from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, and temperature and precipitation changes) best predicted the response (i.e., Shannon diversity change), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). The resulting explicative variables explaining species richness change included the bioclimatic region, land use history, forest cover, protection, past management, recent management, basal area (m^2/ha), temperature and precipitation changes. P values indicating the significant effects are highlighted in bold. The number of plots (NFI plots), R^2 and R^2 adjusted values, and the models' AIC value are also shown.

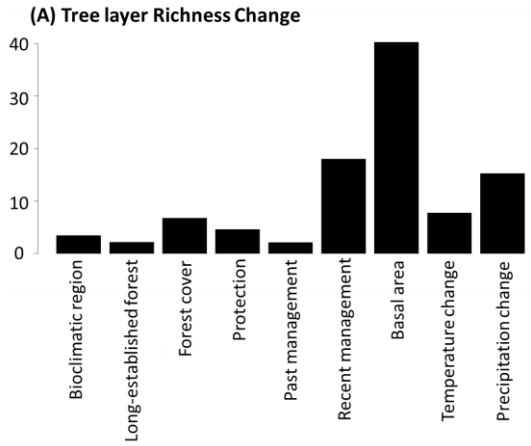
	Regeneration layer Shannon diversity index change		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.01	-0.06 – 0.03	**0.016**
Montane	-0.01	-0.05 – 0.03	0.547
Supramediterranean	-0.02	-0.07 – 0.03	0.483
Long-established forest	0.06	0.01 – 0.11	**0.014**
Forest cover	-0.01	-0.02 – 0.01	0.403
Protection	0.08	0.02 – 0.14	**0.013**

Past management	-0.09	-0.18 – -0.01	**0.036**
Recent management	-0.09	-0.18 – -0.00	**0.044**
Basal area	-0.10	-0.14 – -0.05	**<0.001**
Temperature change	0.06	0.03 – 0.08	**<0.001**
Precipitation change	0.05	0.02 – 0.07	**<0.001**
Observations	3141		
R^2 / R^2 adjusted	5.0% / 4.2%		
Lowest AIC	3602.43		

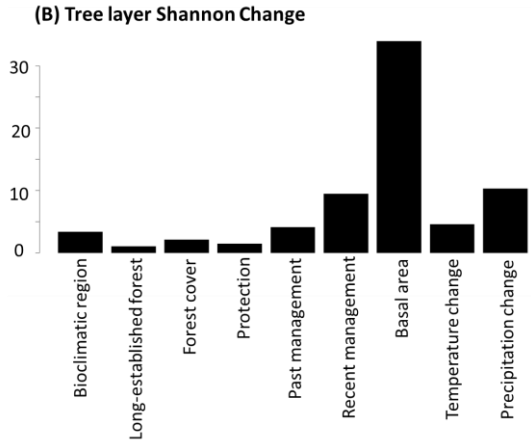
Table S9: Results of the linear model for the Simpson diversity index change from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, temperature and precipitation changes) best predicted the response (i.e., Simpson diversity change), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). The resulting explicative variables explaining species richness change included the bioclimatic region, land use history, forest cover, protection, past management, recent management, basal area (m^2/ha), and temperature and precipitation changes. P values indicating the significant effects are highlighted in bold. The number of plots (NFI plots), R^2 and R^2 adjusted values, and the models' AIC value are also shown.

	Regeneration layer Simpson diversity index change		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.00	-0.06 – 0.05	0.332
Montane	0.05	0.01 – 0.09	**0.017**
Supramediterranean	0.01	-0.05 – 0.06	0.826
Long-established forest	0.02	-0.02 – 0.06	0.255
Forest cover	0.01	-0.01 – 0.03	0.174
Protection	0.01	-0.02 – 0.04	0.512
Past management	-0.04	-0.09 – 0.01	0.132
Recent management	0.06	-0.01 – 0.12	0.084
Basal area	0.02	0.01 – 0.04	**0.011**
Temperature change	0.07	0.04 – 0.10	**<0.001**
Precipitation change	0.01	-0.01 – 0.03	0.297
Observations	3141		
R^2 / R^2 adjusted	2.7% / 1.9%		
Lowest AIC	3726.778		

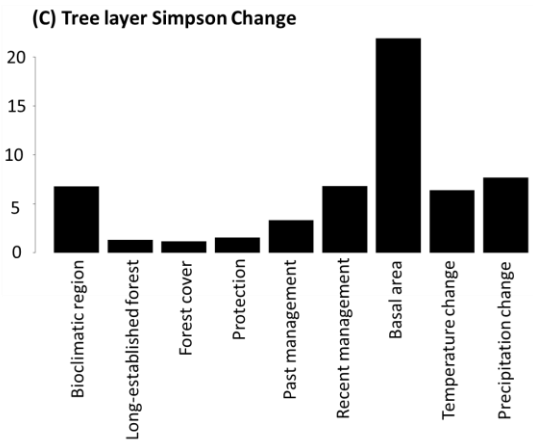
Figure S9. The percentage of variance explained by each variable using the Hierarchical Partitioning method, which shows the goodness of Fit Calculation by randomizing each explicative variable. This method computes the independent and joint contributions of each explicative variable to a linearized regression by hierarchical decomposition of goodness-of-fit measures of regressions (Log-likelihood) using all subsets of predictors in the data set. The Hierarchical Partitioning Randomisation method was used, conducting 499 simulations, to assess the statistical significance of the independent contribution of each variable's effect, using a gaussian function for the case of diversity change models the tree (A,B,C) and regeneration (D,E,F) layers, respectively. LogLik link was used as goodness-of-fit measure. The barplots for each model represent the independent value computed as the percentage of the total explained variance of the effects. The summary tables for each model show the observed I values (i.e., the independent contribution towards explained variance of each variable), the Z-scores for the generated distribution of randomized independent values, and the 95th percentile values of I for the randomized data. "hier.part" R package was used (see Walsh et al., (2020) Package 'hier. part'. *R project for statistical computing*.)



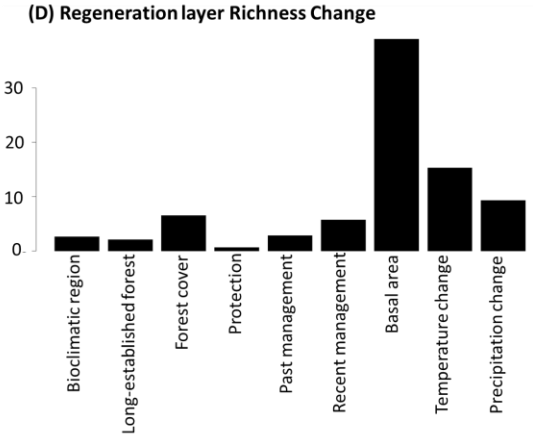
Variable	Obs	Z.score	Sig95
Bioclimatic region	2.53	7.99	*
Long-established forest	1.61	11.03	*
Forest cover	6.33	5.62	n.s.
Protection	0.54	0.15	n.s.
Past management	1.20	8.65	n.s.
Recent management	16.82	81.96	*
Basal area	39.70	189.56	*
Temperature change	7.09	63.97	*
Precipitation change	11.19	21.19	*



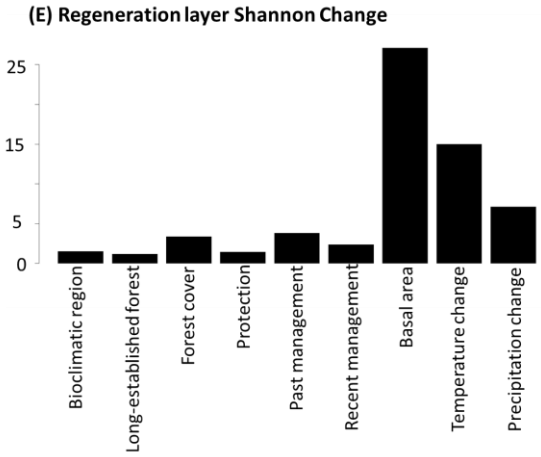
Variable	Obs	Z.score	Sig95
Bioclimatic region	1.31	0.73	*
Long-established forest	0.81	9.15	*
Forest cover	1.37	10.16	n.s.
Protection	0.61	0.97	n.s.
Past management	1.25	0.43	n.s.
Recent management	7.46	11.67	*
Basal area	32.40	36.30	*
Temperature change	3.72	6.92	*
Precipitation change	8.23	14.53	*



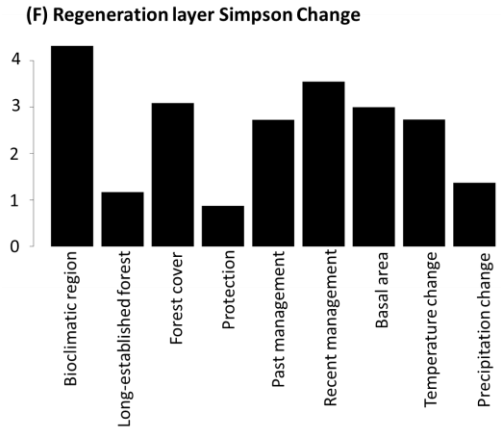
Variable	Obs	Z.score	Sig95
Bioclimatic region	2.03	0.30	*
Long-established forest	0.68	1.53	*
Forest cover	0.38	0.63	n.s.
Protection	0.34	-0.16	n.s.
Past management	0.95	0.14	n.s.
Recent management	4.35	3.04	*
Basal area	21.04	71.50	*
Temperature change	2.27	0.69	*
Precipitation change	5.69	9.21	n.s.



Variable	Obs	Z.score	Sig95
Bioclimatic region	0.66	-0.01	n.s.
Long-established forest	0.78	0.67	*
Forest cover	5.29	12.90	n.s.
Protection	0.31	1.87	*
Past management	2.24	8.56	n.s.
Recent management	4.41	7.54	*
Basal area	37.48	46.18	*
Temperature change	13.38	14.35	*
Precipitation change	7.94	19.20	*



Variable	Obs	Z.score	Sig95
Bioclimatic region	0.47	0.30	n.s.
Long-established forest	0.93	11.64	*
Forest cover	2.41	5.96	n.s.
Protection	0.62	1.01	*
Past management	2.81	25.56	*
Recent management	2.01	22.55	*
Basal area	26.86	211.03	*
Temperature change	12.87	136.49	*
Precipitation change	6.62	36.10	*



Variable	Obs	Z.score	Sig95
Bioclimatic region	3.71	10.80	*
Long-established forest	1.03	27.98	n.s.
Forest cover	0.92	0.32	n.s.
Protection	0.25	0.20	n.s.
Past management	1.06	0.88	n.s.
Recent management	1.95	2.46	n.s.
Basal area	2.61	30.20	*
Temperature change	2.11	5.62	*
Precipitation change	0.91	4.21	n.s.

Table S10: Results of the generalized linear effect model explaining recruitment likelihood from inside (i.e., 1) or outside (i.e., 0) the plots and the role of species functional traits for recruitment from the NFI2 (1989) to the NFI4 (2016) for the tree layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, temperature and precipitation change, and species cluster category) best predicted the response (i.e., recruitment from inside (values tend to 1) and outside the plots (values tend to 0)), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). To evaluate the performance of this binary classification algorithm, we performed the Receiver Operating Characteristic curve (ROC), the Area Under the Curve (AUC) and the brier score (pROC *package*, Robin et al., 2011). The resulting explicative variables included the bioclimatic region, land-use history, forest cover, past management, recent management, temperature and precipitation changes, and species' cluster classification. P values indicating the significant effects are highlighted in bold. The number of observations (i.e., each recruited species), the R^2 value, the Receiver Operating Characteristic (ROC), the Area Under the Curve (AUC), the Brier score value, and the models' AIC value are shown. Note that for applying the generalized linear model with binomial distribution, the "inside" and "outside" variable levels were converted to 1 and 0, respectively. Cluster classifications correspond to: Cluster 1 = animal dispersed species with lower drought tolerance and higher shade tolerance; Cluster 2 = animal dispersed species with relatively higher drought tolerance and lower shade tolerance; Cluster 3 = species with other dispersal methods with relatively lower drought tolerance and higher shade tolerance; and Cluster 4 = species with other dispersal methods and relatively higher drought tolerance and lower shade tolerance.

	Tree layer species recruitment patterns		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.16	0.06 – 0.33	**<0.001**
Montane	1.01	0.42 – 2.66	0.983

Supramediterranean	0.65	0.19 – 2.10	0.473
Long-established forest	1.22	0.93 – 1.59	0.151
Forest cover	1.23	1.09 – 1.40	**0.001**
Past management	1.00	0.31 – 3.05	1.000
Recent management	0.68	0.32 – 1.28	0.265
Temperature change	1.10	0.72 – 1.69	0.654
Precipitation change	1.08	0.75 – 1.54	0.686
Cluster [1]	1.55	0.40 – 5.69	0.510
Cluster [2]	3.17	1.48 – 7.64	**0.005**
Cluster [4]	1.17	0.48 – 3.11	0.743
Observations	1947		
R^2	13.51%		
ROC - AUC	0.68		
Brier score	0.18		
Lowest AIC	2146.84		

Table S11: Results of the generalized linear effect model explaining recruitment likelihood from inside (i.e., 1) or outside (i.e., 0) the plots and the role of species functional traits for recruitment from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer. To determine which explicative variables (i.e., bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, temperature and precipitation changes, and species cluster category) best predicted the response (i.e., recruitment from inside (values tend to 1) and outside the plots (values tend to 0)), we used the Stepwise Algorithm from the R package MASS (Ciaburro, 2018). To evaluate the performance of this binary classification algorithm, we performed the Receiver Operating Characteristic curve (ROC), the Area Under the Curve (AUC) and the brier score (pROC *package*, Robin et al., 2011). The resulting explicative variables included the bioclimatic region, land-use history, forest cover, protection, past management, basal area, temperature and precipitation changes, and species' cluster classification. P values indicating the significant effects are highlighted in bold. The number of observations (i.e., each recruited species), the R^2 value, the Receiver Operating Characteristic (ROC), the Area Under the Curve (AUC), and the Brier score value, and the models' AIC value are shown. Note that for applying the generalized linear model with binomial distribution, the "inside" and "outside" variable levels were converted to 1 and 0, respectively. Cluster classifications correspond to: Cluster 1 = animal dispersed species with lower drought tolerance and higher shade tolerance; Cluster 2 = animal dispersed species with relatively higher drought tolerance and lower shade tolerance; Cluster 3 = species with other dispersal methods with relatively lower drought tolerance and higher shade tolerance; and Cluster 4 = species with other dispersal methods and relatively higher drought tolerance and lower shade tolerance.

	Regeneration layer species recruitment patterns		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.10	0.03 – 0.27	**<0.001**
Montane	0.34	0.15 – 0.76	**0.010**

Supramediterranean	0.45	0.11 – 1.63	0.246
Long-established forest	0.60	0.34 – 1.05	0.069
Forest cover	1.83	0.80 – 4.83	0.182
Protection	1.42	0.97 – 2.07	0.072
Past management	0.40	0.04 – 2.53	0.371
Basal area	1.53	0.94 – 2.49	0.083
Temperature change	0.92	0.65 – 1.31	0.630
Precipitation change	0.84	0.65 – 1.09	0.187
Cluster [1]	2.07	0.68 – 6.79	0.206
Cluster [2]	2.11	0.95 – 5.72	0.098
Cluster [4]	62.08	25.43 – 181.31	**<0.001**
Observations	1184		
R^2	38.10%		
ROC - AUC	0.86		
Brier score	0.12		
Lowest AIC	992.46		

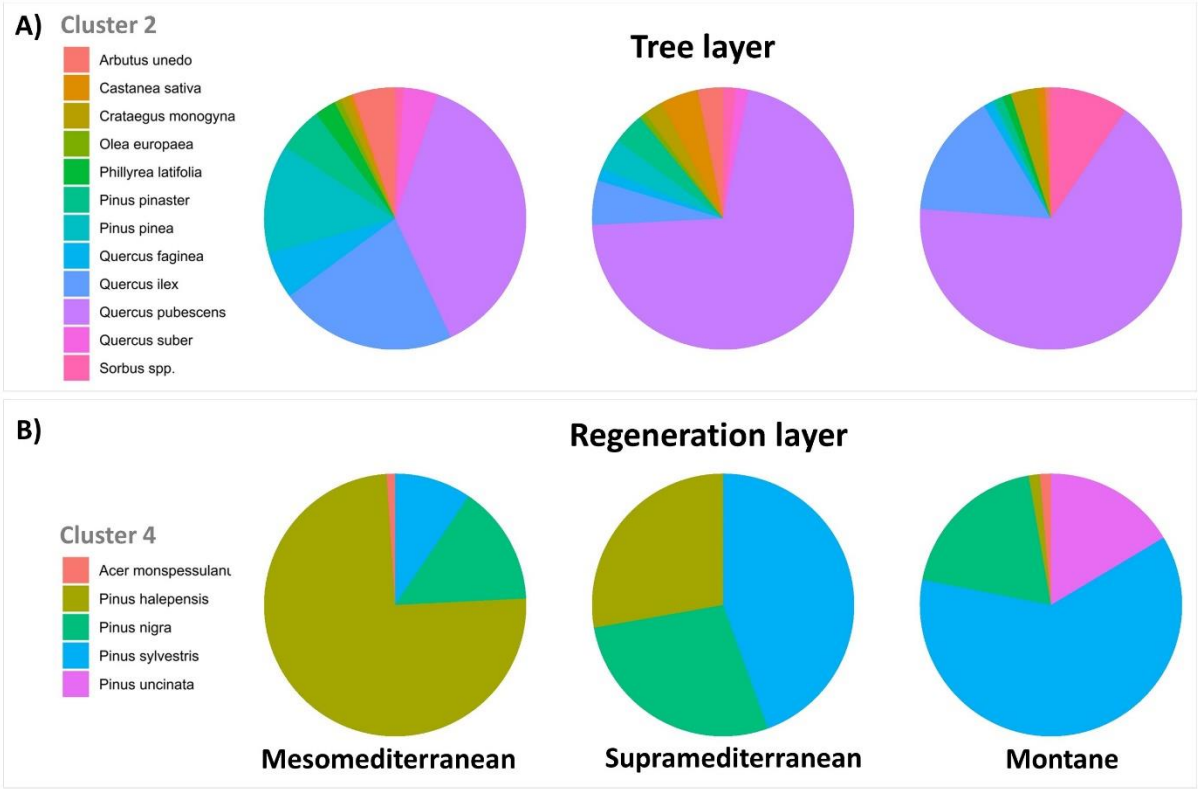


Figure S10. Distribution of those newly recruited species according to the three bioclimatic regions studied for (A) the tree layer and those animal-dispersed, higher drought and lower shade tolerant species (Cluster 2), and (B) the regeneration layer and those species dispersed by other methods, higher drought and lower shade tolerant (Cluster 4).

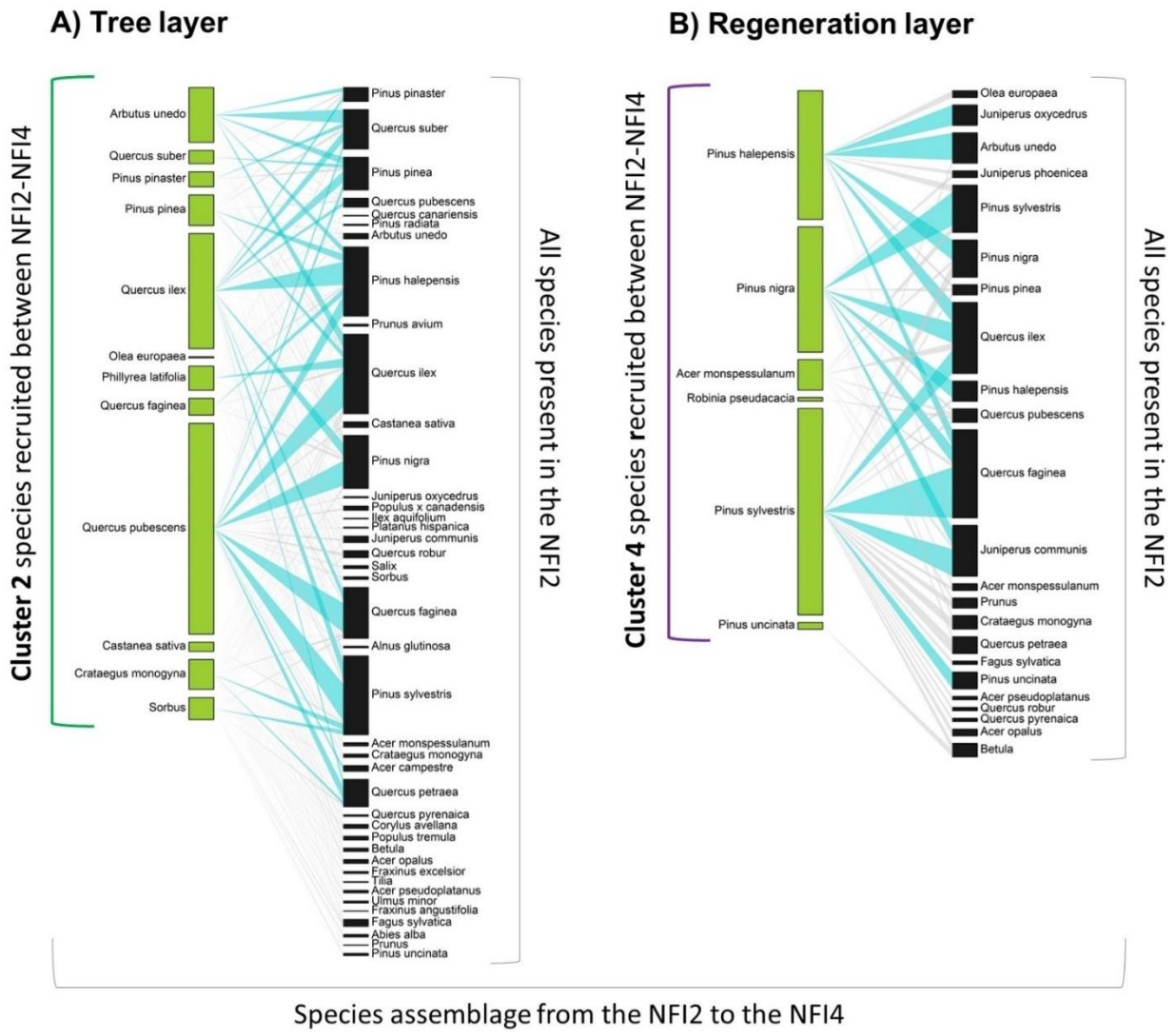
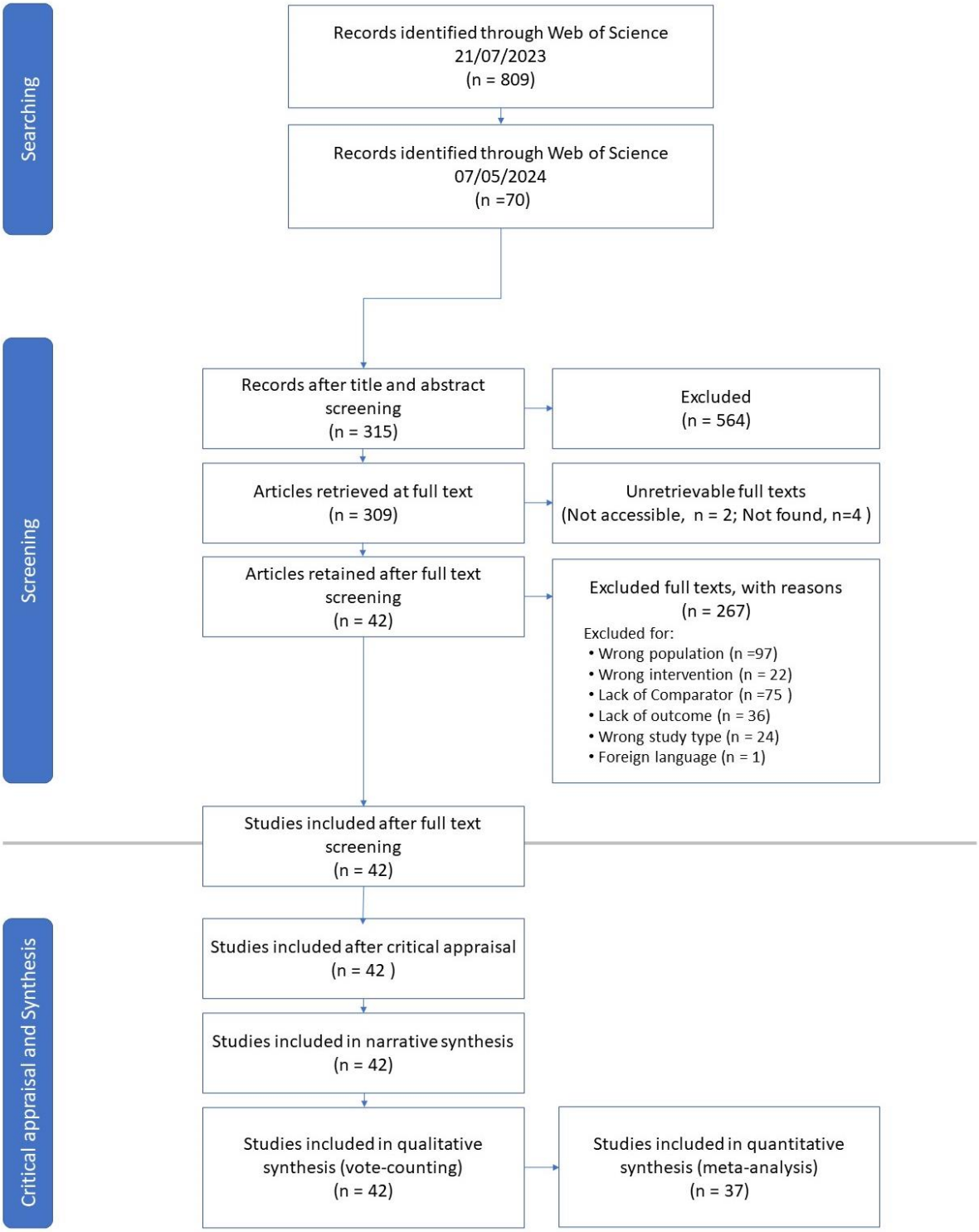


Figure S11. Species assemblage in the NFI4 plots (2016) resulting from the sum of the incorporation of new species (green bars) recruited together with those species already present in the NFI2 (1989) inventory (black bars). Figure A represents for the tree layer the new assemblage of those animal-dispersed species with higher drought tolerance (i.e., Cluster 2) significantly recruited from outside the plots during the period between the NFI2-NFI4. While Figure B represents for the regeneration layer the new assemblage of those species dispersed by other methods with higher drought tolerance (i.e., Cluster 4) significantly recruited from inside the plots during the period between the NFI2-NFI4. The size of bars represents species counts for all plots in which diversity increased. The size of the connectors (grey and blue links) indicates the number of plots in which the new species were recruited. Specifically, blue connectors indicate more than 15 counts for the tree layer, and 5 counts for the regeneration layer.

Appendix 3

Supplementary material – Chapter 4

Supplement S1. Reporting standards for Systematic Evidence Syntheses (ROSES) flow diagram showing literature searching and inclusion/exclusion process as used in this study. Adapted from Haddaway et al. (2018).



Supplement S2. Glossary for the complete list of variables extracted from the primary studies selected.

General article characteristics

DOI: reference information for each study.

Publication year: the year of publication.

Study design: methodological approach for each study categorized into experimental, observational, satellite data or simulation.

Country: geographical location of the study.

Coordinates: geographical position of each study site **(**x and y coordinates).

Biome: As biome information was not standardized across papers, we classified the study cases for climate based on the geographic position of the study site using the global Köppen-Geiger climate classification map (http://koeppen-geiger.vu-wien.ac.at/present.htm). This resulted in temperate forests, mediterranean woodlands, temperate and subtropical grasslands/savannas, tropical/subtropical forests, and boreal/montane forests

Ecosystem type: categorized into forest or grassland ecosystems as reported in the primary studies.

Spatial scale: area undergone rewilding treatment: site (10-1000m2), local (1-10km2), landscape (10-200km2), regional (200-2000km2), and global (> 10000km2).

Temporal scale: time since rewilding treatment measured in years.

Rewilding data

Previous degradation: past land use or disturbance for each study site (i.e., agriculture practices, livestock overgrazing, mining, fire, presence of invasive species) for which rewilding passively or actively occurred.

Rewilding type: categorized into passive (e.g., allowing natural succession after land abandonment or after disturbances) or active (see Rewilding interventions below).

Rewilding components: consisted of the three rewilding components proposed by Perino et al. (2019) (i.e., trophic complexity, disturbance stochasticity and dispersal) to promote self-regulating complex ecosystems by restoring non-human ecological processes while reducing human control and pressures.

Rewilding interventions: specific rewilding interventions reported for each study. Rewilding interventions were further categorized into three rewilding components (biodiversity, disturbances, connectivity) similar to the those described by Perino et al. (2019), namely, trophic complexity, disturbance stochasticity and dispersal. Thus, we considered a rewilding intervention to target trophic complexity when the outcome increased compositional or functional complexity (e.g., increase in biodiversity). We considered a rewilding intervention to target stochastic disturbance when the outcome released ecosystems from continued and controlled anthropogenic disturbances (e.g., restoration of semi(natural) fire regimes). We considered a rewilding intervention to target dispersal when the outcome improved connectivity among habitats allowing for dispersal of species (e.g., reduce landscape fragmentation).

- Specific rewilding interventions which targeted trophic complexity were animal introduction, animal removal, herbivory enclosure, invasive or non-native plant removal, plant introductions, animal protection, and plant protection.

- Specific rewilding interventions which targeted disturbance stochasticity were the use of prescribed fire or grazing.

- Specific rewilding interventions which targeted trophic complexity/disturbance stochasticity were any of the above trophic complexity and disturbance stochasticity interventions combined.

- Specific rewilding interventions which targeted trophic complexity/dispersal were animal introduction and animal removal.

Specific species managed: categorization of the species managed into: (i) wild, domestic, or invasive animals and their ecological guild (i.e., carnivores, herbivores, omnivores), and (ii) native or invasive plants and plantation forests, and their life forms (i.e., trees, shrubs, herbs).

Disturbance data

Specific disturbance: specific disturbances reported for each case study. Abiotic disturbances included drought and fire, biotic disturbances included intense herbivory, pests and invasive species.

Disturbance agent: specific disturbances categorized whether disturbances were generated by abiotic, or nonliving, forces such as weather and wildfires, or as a result of biotic, or living, forces such as invasions of exotic species and pests.

Disturbance type: as disturbance can vary in their frequency and intensity, we generally categorized them as reported in the primary studies, as:

- Episodic disturbances: infrequent but often intense events that cause significant changes in the ecosystems assessed.

- Gradual disturbances: disturbances that occur slowly over extended periods.

- Recurrent disturbances: regular and sometimes predictable events that occur at relatively consistent intervals.

Resilience data:

Resilience approach:

- Engineering resilience: recovery of a system to its previous undisturbed state (reference state) (Pimm, 1984) as stated in the primary studies.
- Ecological resilience: maximum change that a system can absorb without shifting to an alternative state (Holling, 1973) as stated in the primary studies.

- Socio-ecological resilience: capacity of a socio-ecological system to reorganize, adapt and provide ecosystem services after disturbance (Folke, 2006) as stated in the primary studies.

Resilience dimension: resistance, recovery, and resilience concepts were used to describe how each study system responded to the disturbance event (see Lloret et al., 2024; Van Meerbeek et al., 2019), as reported in the primary studies.

- Resistance: the ability of the system to withstand disturbances without undergoing significant changes in its structure and function.
- Recovery: the ability of the system to return to its pre-disturbance state following disturbance. It involves the re-establishment of species, community structure, and ecosystem functions.
- Resilience: the capacity of a system to absorb disturbances, reorganize, and continue to function in a similar way. It encompasses both resistance to change and the ability to recover after disturbances.

System variable: system variables correspond to the measured variables reported in each primary study, for which resilience is quantified. As described in the ORF (Lloret et al. 2024), resilience of a system is estimated by comparing the state of these system variables modified by disturbances or stressors in comparison to values (i.e., reference state) that correspond to the absence of disturbance or stress, or, alternatively, to situations in which the variables remain within acceptable thresholds. The closer the variables of the system affected by disturbances or stressors get to these reference values, the greater is the resilience.

Owing to the large number of different system variables recorded in theprimary studies, they were classified into four broader types of categories, namely, (i) individual characteristics and demographic processes, (ii) compositional, trophic, and functional biodiversity, (iii) biophysical characteristics and structure and (iv) characteristics of the disturbance regime. See Table 2 in the main text for the list of the system variables included in the classification.

Supplement S3: Model selection based on backward elimination of moderator variables that may explain the effects of rewilding on ecosystem resilience. AICc corresponds to the corrected Akaike's information criterion for small samples, and ΔAICc corresponds to the relative difference in AICc values from the model with the smallest AICc. Notice that models showing ΔAICc >4 are generally considered to have weaker support relative to the best model (i.e., the one with the lowest AIC).

Model	**AICc**	**ΔAICc**
System variable category + (1 | ID)	1539.93	0.00
System variable category + Disturbance type + (1 | ID)	1541.79	1.86
System variable category + Disturbance type + Resilience approach + (1 | ID)	1542.51	2.58
System variable category + Disturbance agent + Disturbance type + Resilience approach + (1 | ID)	1542.35	2.42
System variable category + Disturbance agent + Disturbance type + Resilience approach + Resilience dimension + (1 | ID)	1544.23	4.30
System variable category + Disturbance agent + Disturbance type + Resilience approach + Resilience dimension + Ecosystem type + (1 | ID)	1546.16	6.23

Supplement S4. Chi-squared tests (χ^2) indicating significant differences among the three directional effects (i.e., positive, neutral and negative effects) on ecosystem resilience for (A) rewilding components, (B) system variable categories and (C) the most representative trophic rewilding interventions.

Variables	N	χ^2	p-value
(A) Rewilding component			
Trophic-Disturbance-Trophic/disturbance	305	169.9	<0.001
Trophic	195	131.35	<0.001
Disturbance	49	9.34	0.007
Trophic/disturbance	61	57.67	<0.001
(B) System variable category			
Demography	114	67.41	<0.001
Biodiversity	34	12.76	0.001
Biophysical	81	33.18	<0.001
Disturbance	76	68.07	<0.001
(C) Trophic rewilding interventions			
Animal introduction	63	52.95	0.001
Animal removal	22	6.54,	0.01
Plant introduction	50	28.84	0.001
Plant removal	67	34.59	0.001

Supplement S5. Overall effect size and effect size for each group of moderators considering the effects of rewilding components simultaneously (trophic, disturbance, and trophic/disturbance) on ecosystem resilience. Effect sizes were calculated using Hedges'g. Standard error distributions (± se) and p-values are shown. High heterogeneity among observations was observed (Q_{Total}=8813.62, p<0.001). I^2, Q_M and significant level values for each group of moderators are also shown. I^2 represents the percentage of variation due to heterogeneity, Q_M corresponds to heterogeneity among moderators and p-value is the level of significance among effect sizes of factor levels.

	Effect size	± se	p-value
Overall	1.08	0.30	<0.001
System variable			
Demography	0.84	0.31	<0.01
Biodiversity	1.05	0.33	<0.01
Biophysical	0.80	0.31	<0.05
Disturbance	1.59	0.31	<0.001
(I^2 = 3.37%; Q_M = 88.54; p<0.001)			
Resilience approach			
Engineering	1.74	0.49	<0.01
Ecological	0.94	0.47	<0.05
Socio-ecological	0.46	0.77	>0.05
(I^2 = 3.43%; Q_M = 13.39; p<0.01)			
Resilience dimension			
Resistance	0.70	0.57	>0.05
Recovery	1.26	0.86	>0.05
Resilience	1.24	0.41	<0.01
(I^2 = 3.49%; Q_M = 12.47; p<0.05)			
Disturbance agent			
Biotic	2.09	0.40	<0.01
Abiotic	-0.87	0.41	<0.05
(I^2 = 5.51%; Q_M = 314.65; p<0.001)			
Disturbance type			
Episodic	0.30	0.44	>0.05
Gradual	1.60	0.43	<0.001
Recurrent	1.21	0.52	<0.05

(I^2 = 5.34%; Q_M = 306.7; p<0.001)			
Ecosystem type			
Forest	0.98	0.42	<0.05
Grassland	1.19	0.46	<0.01
(I^2 = 3.43%; Q_M = 12.13; p<0.01)			

Supplement S6. Overall effect size and effect size for each system variable category for (A) trophic, (B) disturbance, and (C) trophic/disturbance rewilding components on ecosystem resilience. Effect sizes were calculated using Hedges'g. Standard error distributions (± se) and p-values are shown. High heterogeneity among observations was observed for trophic (Q_{Total}=6338.92, p<0.001), disturbance (Q_{Total}=5780.92, p<0.001) and trophic/disturbance (Q_{Total}=1795.33, p<0.001) rewilding components. I^2, Q_M and significant level values for each group of system variable categories are also shown. I^2 represents the percentage of variation due to heterogeneity, Q_M corresponds to heterogeneity among moderators and p-value is the level of significance among effect sizes of factor levels.

	Effect size	± se	p-value
(A) Trophic			
Overall	1.01	0.38	<0.001
Demography	0.80	0.39	<0.05
Biodiversity	0.45	0.42	>0.05
Biophysical	0.98	0.39	<0.05
Disturbance	1.41	0.39	<0.001
(I^2 = 4.02%; Q_M = 38.98; p<0.001)			
(B) Disturbance			
Overall	1.07	0.45	<0.05
Demography	0.81	0.51	>0.05
Biodiversity	1.56	0.60	<0.01
Biophysical	0.83	0.50	>0.05
Disturbance	1.25	0.51	<0.05
(I^2 = 1.17%; Q_M = 38.9; p<0.01)			
(C) Trophic/disturbance			
Overall	1.68	0.56	<0.01
Demography	1.31	0.58	<0.05
Biodiversity	2.54	0.62	<0.001
Biophysical	1.13	0.59	>0.05
Disturbance	3.09	0.59	<0.001
(I^2 = 2.24%; Q_M = 112.8; p<0.001)			

Supplement S7. Overall effect size and effect size for each specific trophic rewilding intervention on ecosystem resilience. Effect sizes were calculated using Hedges'g. Standard error distributions (± se) and p-values are shown. High heterogeneity among observations was observed (Q_{Total}=6419.54, df=189, p<0.001). I^2, Q_M and significant level values for each group of interventions are also shown. I^2 represents the percentage of variation due to heterogeneity, Q_M corresponds to heterogeneity among moderators and p-value is the level of significance among effect sizes of factor levels.

	Effect size	**± se**	**p-value**
Overall	1.04	0.42	<0.05
Animal introduction	1.19	0.47	<0.05
Animal removal	0.26	1.10	>0.05
Plant introduction	1.16	0.57	<0.05
Plant removal	1.18	0.48	<0.05
(I^2 = 4.53%; Q_M = 5942.34; p<0.001)			

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