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REVIEW ARTICLE

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

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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.

Key words: active and passive restoration, frugivory, functional restoration, plant–animal interactions, tropical and temperate forests

Conceptual Implications

- Animal-mediated seed dispersal is a key process to ensure forest restoration success in both tropical and temperate biomes.
- 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.
- Plant dispersal syndromes and seed disperser traits are the most relevant intrinsic factors determining restoration success stressing the importance of actions to ensure their matching.
- Our review suggests that strategies differing in their effort may be needed in temperate and tropical biomes to ensure restoration success.

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 (Kurten 2013; Bello et al. 2015). 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) (Crouzeilles et al. 2016; Meli et al. 2017; Aronson et al. 2020). Although a critical need to assess the outcomes of forest restoration actions

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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 (Ruiz-Jaen & Aide 2005; Forup et al. 2008; Brudvig 2011) 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; Jordano & Godoy 2002; Forget et al. 2011). Within seed dispersal mechanisms, we chose to focus on animal-mediated seed dispersal, provided by the interactions between fruiting plants and frugivorous animals (Jordano & Godoy 2002; Forget et al. 2011). 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 (Traveset et al. 2007; Rubalcava-Castillo et al. 2021). 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; Viani et al. 2015; Rubalcava-Castillo et al. 2021). 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 (Howe & Smallwood 1982; Herrera 1984).

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 (Orrock et al. 2006; Kuprewicz 2013; Naoe et al. 2018). 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), microsite 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; Molin et al. 2018; Koelemeijer et al. 2021).

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 (Clark et al. 1999; Aide et al. 2013). 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.

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 and 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 nondegraded) 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 above-mentioned 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 three 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 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 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. 1 and 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 (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 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 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 Supplement S2 for a more detailed rationale of the classification of forest restoration success.

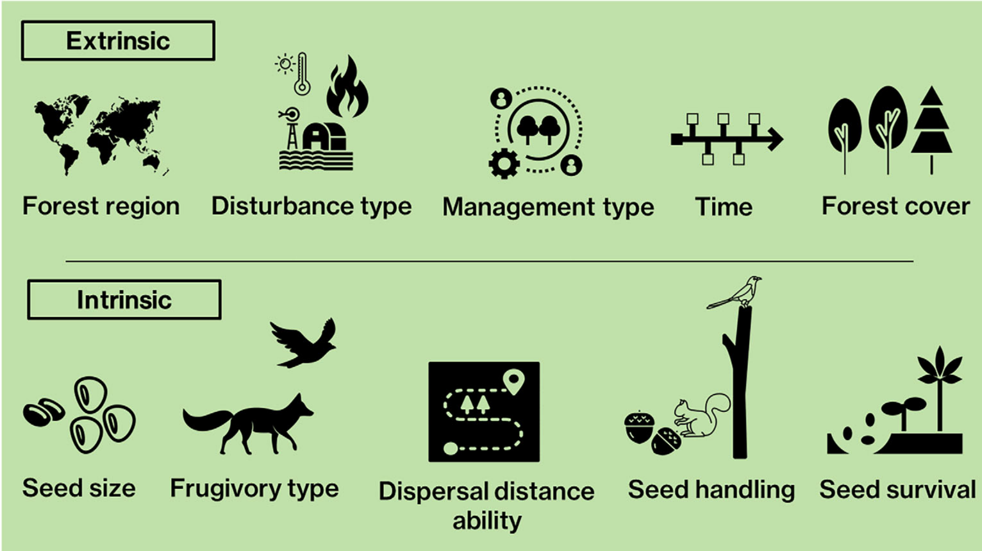

Figure 1. Main intrinsic and extrinsic dispersal factors used to evaluate forest restoration success by means of animal-mediated seed dispersal. See Supplement S2 for complete list of variables and descriptions.

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. Second, to investigate how intrinsic and extrinsic dispersal factors may drive restoration success, we conducted two complementary analyses. First, 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, $\cos^2$) 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). Second, 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 & Wickham 2017), rpart (Therneau et al. 2015), and FactoMineR (Husson et al. 2016).

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 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 Supplement S3).

Regardless of the type of biome, extrinsic factors were slightly more addressed in the reviewed articles (Supplement

S3; Table S2). Moreover, all extrinsic factors were similarly used aside from microenvironmental 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 (Supplement S3; Table S2).

Drivers of Restoration Success

Globally, the two-way CA explained 92.6% of the cumulative variance ($\chi^2 = 536.90$; $p = 2.62 \times 10^{-20}$) in the patterns of restoration success, including all intrinsic and extrinsic dispersal factors. The $\cos^2$ quality of representation test showed that most variables were highly represented by these two dimensions (Supplement S4). 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 microenvironmental 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; Supplement S4). Contrarily, frugivory by rodents contributed to "unsuccessful" restoration efforts (Fig. 2; Supplement S4).

For the two-way CA of tropical (Cumulative % of var. = 88.7; $\chi^2 = 448.63$; $p = 9.77 \times 10^{-12}$) and temperate systems (Cumulative % of var. = 84.6; $\chi^2 = 203.40$; $p = 0.98$), most variables were also highly represented by the first two dimensions (Figs. 3 & 4; Supplement S4). For both tropical and temperate biomes (Figs. 3 & 4; Supplement S4), 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" microenvironmental 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. 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. 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. 3 & 4). Within the variables which contributed the most to a "low" and "unsuccessful" restoration, we found few differences between biome types (Figs. 3 & 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. 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. 4).

For all biome types, the classification tree layout showed that the overall probability of restoration success was 81% (Supplement S3) 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" microenvironmental 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 (Supplement S5).

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 (Supplement S5). Extrinsic factors that showed major importance in the effective restoration outcome of tropical forests were higher restoration age, "improvement" of microenvironmental conditions, having a close reference habitat and an assisted or reconstructive restoration approach (Supplement S5), while only "frequent" or "continuous" forest cover was relevant for temperate biomes (Supplement S5). 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 (Supplement S5) while lack of hoarder activity and "high" animal dispersers abundance were relevant in temperate ones (Supplement S5).

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

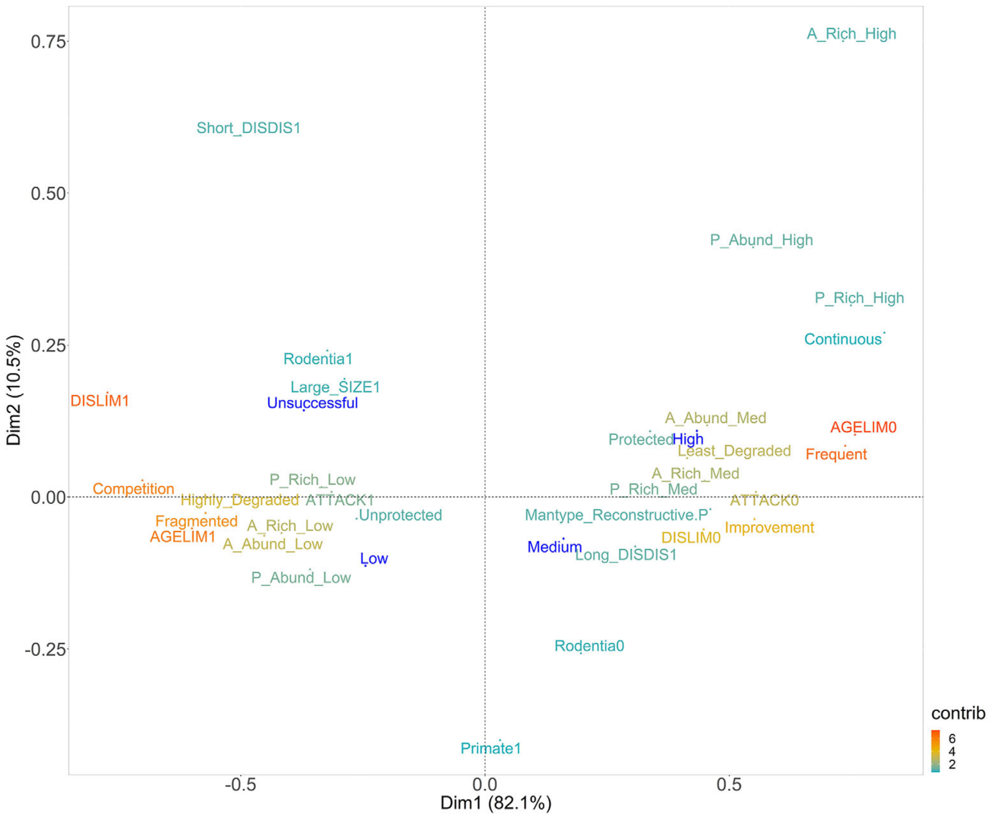

Figure 2. Variable contribution for "high," "medium," "low," and "unsuccessful" restoration success (blue labels) in all biomes, defined by two-way correspondence analysis (see Supplement S2 and Table S1 for variable codes and descriptions). Only the 32 variables with the highest contribution are shown.

provide are becoming more widespread (Pereira & Navarro 2015; Ockendon et al. 2018; 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 socioeconomic 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., Vallejo et al. 2012; Crouzeilles et al. 2016; O'Donnell et al. 2018). 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).

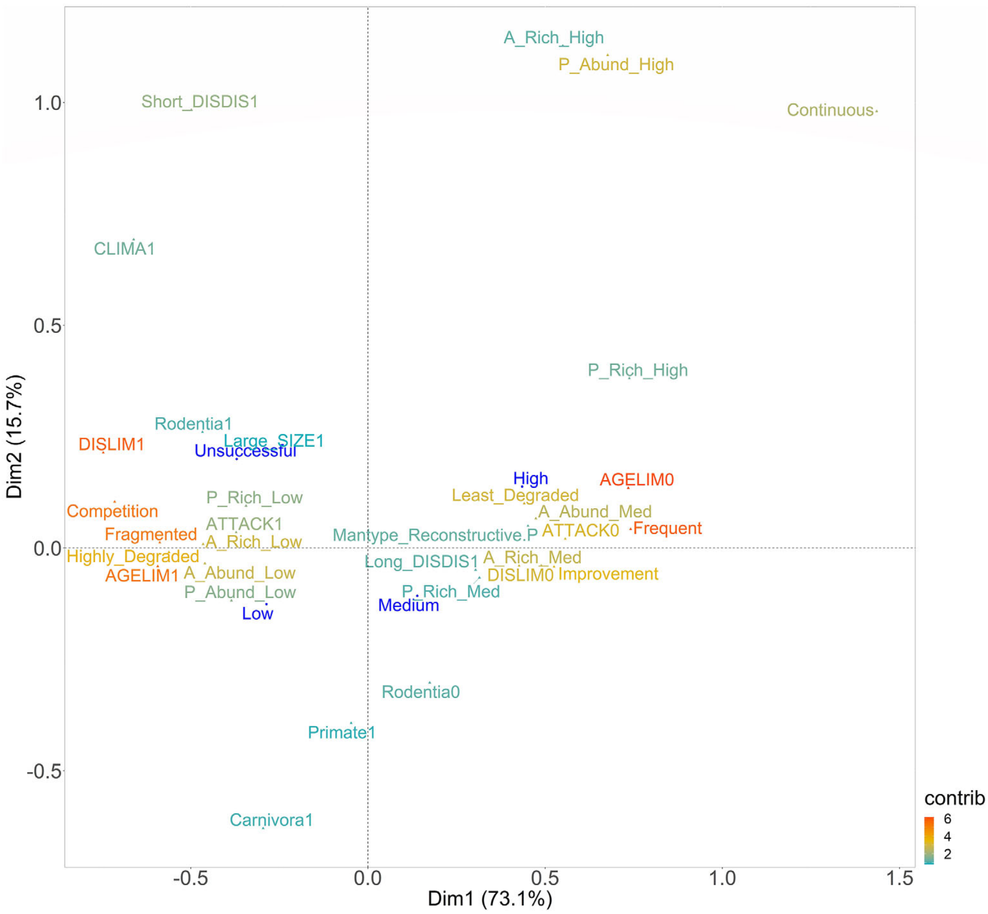

Figure 3. Variable contribution for “high,” “medium,” “low,” and “unsuccessful” restoration success (blue labels) in tropical biomes, defined by two-way correspondence analysis (see Supplement S2 and Table S1 for variable codes and descriptions). Only the 32 variables with the highest contribution are shown.

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 (González-Varo et al. 2013; Selwyn et al. 2020; Rubalcava-Castillo et al. 2021). 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 (Wright et al. 2000; Galetti et al. 2015). 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 (Wright et al. 2000; Wotton & Kelly 2012). Regarding temperate forests, “small” and “medium-sized” seeds

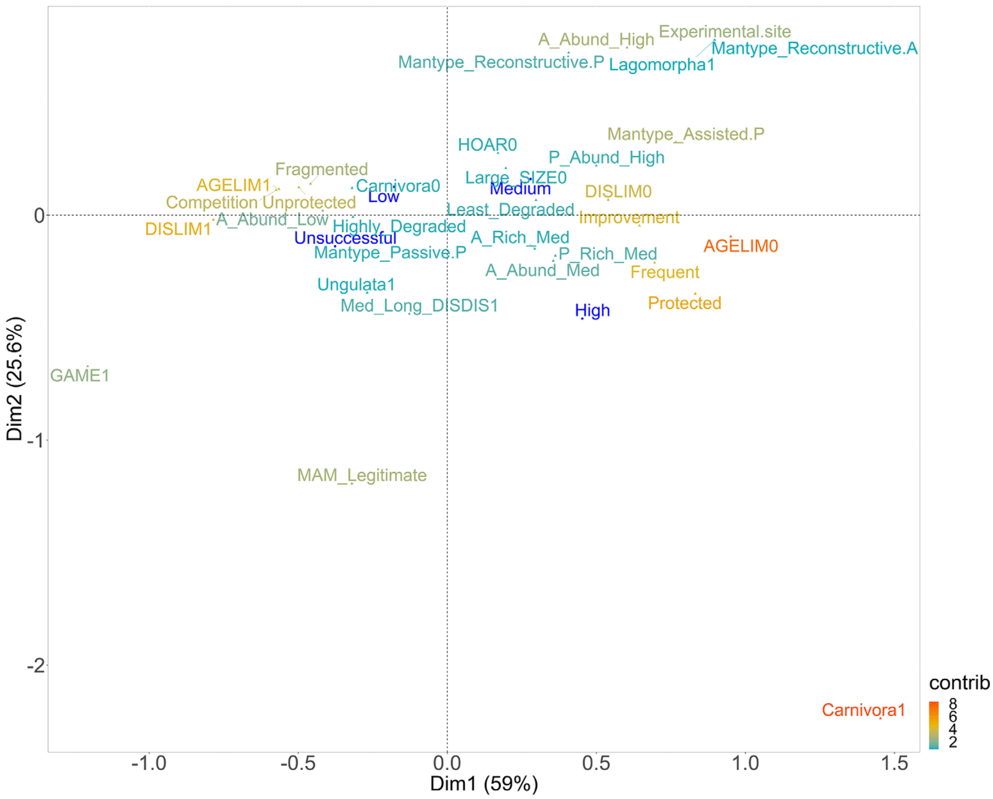

Figure 4. Variable contribution for "high," "medium," "low," and "unsuccessful" restoration success (blue labels) in temperate biomes, defined by two-way correspondence analysis (see Supplement S2 and Table S1 for variable codes and descriptions). Only the 32 variables with the highest contribution are shown.

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 socioeconomic 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 (Shoo et al. 2016; Holl 2017; Mittelman et al. 2020) 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 (Rey-Benayas et al. 2015; Cruz-Alonso et al. 2019; Martínez-Muñoz et al. 2019) 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., Prach & del Moral 2015; Meli et al. 2017).

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.

In addition, 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 microenvironmental 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; Sarmiento et al. 2017; Kulikowski et al. 2022).

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 favor 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.

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.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Codes and descriptions for intrinsic and extrinsic dispersal factors.
Table S2. Usage of intrinsic and extrinsic dispersal factors used to assess forest restoration for all publications, within each type of biome studied.
Supplement S1. Number of publications by biome, continent, and country and geographic representativeness of the study area.
Supplement S2. Description of variables.
Supplement S3. Evolution of publications over time, disturbance categories, and most addressed intrinsic and extrinsic factors.
Supplement S4. Quality of representation tests and variable contributions of the Correspondence Analysis.
Supplement S5. Classification Tree Analysis layout.

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