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Research article

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

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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 (70% of observations). 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 social-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 (social-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 ecosystems for the uncertain effects of increasing climate change and associated disturbances yet acknowledging some limitations depending on the nature of the disturbance.

1. 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 EU Nature Restoration Law (2024) (European Commission, 2023), are examples of awareness and efforts to mitigate climate change impacts while

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simultaneously protecting and rehabilitating natural habitats facing uncertain ecological scenarios.

Rewilding, a concept initially developed in the circles of conservation biology (Soulé and 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 and 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, shifting efforts to restore more natural fire regimes would be an appropriate response. 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 and 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 new 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 and Noss, 2021; Navarro and Pereira, 2015; Svenning, 2020), yet this statement is to date based on indirect assumptions or inferences and not on comprehensive empirical evidence. There is a need to consolidate scattered evidence from diverse case studies across terrestrial ecosystems affected by various disturbance types. Meta-analytical approaches are particularly well-suited to synthesize this evidence (Stewart, 2010) identify trends in demographic processes, biodiversity patterns, biophysical characteristics, and disturbance control, and assess the potential benefits of rewilding for enhancing 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 study aimed to evaluate the effectiveness of rewilding projects considering their potential for ecosystem resilience to disturbances. Specifically, we conducted a thorough analysis of the available scientific literature to assess how well rewilding efforts that focus on increasing trophic complexity, promoting stochastic disturbances, or enhancing dispersal may contribute to improve ecosystem resilience to disturbances. With our findings, we aim to provide evidence-based suggestions to help guide future rewilding efforts in a time of increasing disturbances.

2. Methods

2.1. A unifying framework to assess resilience in rewilding projects

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. Following Perino et al. (2019) we considered a rewilding intervention to target: (i) *trophic complexity* when the aim was to increase structure and interactions across different trophic levels (e.g., by introducing or removing particular animal or plant species) hereafter referred more broadly as "*biodiversity*" to also encompass changes not exclusively related to trophic levels (i.e., genetic, compositional, and functional diversity), (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 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 surpassing a threshold and shifting to an alternative state (Holling, 1973), and (iii) *social-ecological resilience*: capacity of a social-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., Sasaki et al., 2015; Nikinmaa et al., 2023; Lloret et al., 2024). Here, we focus specifically on the operational resilience framework (ORF) developed by Lloret et al. (2024) which recognizes and relates several elements, including: (i) the resilience approach (i.e., engineering, ecological, social-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 "resilience predictors" (*sensu* Lloret et al. (2024)) which are factors that influence the resilience outcome of a system and can be modified or managed to enhance it (see Lloret et al. (2024) for a more extensive description). To connect the two abovementioned theoretical frameworks (rewilding – resilience), the resilience predictors in Lloret et al. (2024) are identified as the manageable interventions aimed at restoring the three rewilding components defined by Perino et al. (2019): biodiversity, stochastic disturbance and connectivity (Fig. 1), assuming that changes in these three targets may modify the resilience of the ecosystem. Although there are different ways to quantify resilience (Nikinmaa et al., 2023), in the ORF, resilience is quantified by analyzing the response of specific system variables that represent key aspects of the system's functionality to disturbances compared to a reference state. The reference state in this context represents a scenario used as a baseline for comparing the system's state after experiencing disturbances or stress (Grimm and Wissel, 1997). This reference state can be partially understood as the range of system variable values that define the basin of attraction, which is separated from other alternative states by thresholds (Scheffer et al., 2001; Sasaki et al., 2015). In our research, the reference state corresponds to the desired state to be achieved while the comparison of the rewilded and the non-rewilded situations, both under disturbance, is used to measure the resilience outcome of the rewilding actions applied (see next section).

2.2. Data acquisition

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) rewilding interventions focusing on enhancing biodiversity, disturbance stochasticity, connectivity, or a combination of these resilience predictors (ii) areas that experienced either passive rewilding (e.g., spontaneous vegetation regeneration after land abandonment) or active rewilding interventions, and subsequently suffered a disturbance or stressor, (iii) control area that did not experience rewilding and experienced the same disturbance or stressor as that in the rewilding intervention, (iv) measurement and comparison of the system variable values in rewilded and non-rewilded areas after disturbance considering a reference state.

To address our research question, we searched published articles on July 21, 2023 and updated our search on May 07, 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 Supplement 1).

2.3. 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) (Supplement 2 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,

Table 1
Classification of rewilding interventions extracted from the primary studies according to the three rewilding components considered. Note that the different rewilding components may be addressed simultaneously.

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, soil disturbance	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)

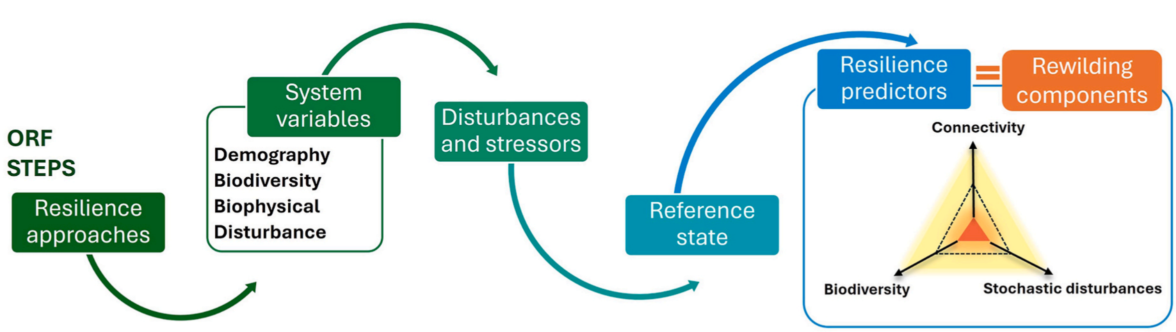

Fig. 1. Representation of the coupling and unification of the two frameworks of Lloret et al. (2024) addressing resilience and Perino et al. (2019) addressing rewilding. The Operational Resilience Framework (ORF) steps shown here correspond to a simplified version of the roadmap to assess resilience 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) of rewilding interventions to promote self-regulating complex ecosystems as defined by Perino et al. (2019).

(ii) stochastic disturbance, and (iii) connectivity (Table 1). When a case study targeted more than one rewilding component, they were all considered. We did not find any study which targeted the connectivity component alone, and therefore, due to the lack of representativeness, the three studies targeting the biodiversity/connectivity component together were included in the biodiversity component. The 45 system variables recorded (Table 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 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 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, %, counts.	(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

2.4. Data analysis

2.4.1. Qualitative analysis (vote counting and classification tree analysis)

We first compiled, described and catalogued the available studies (James et al., 2016) on rewilding 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 and Smith (2012). Rewilding interventions that significantly influenced resilience when compared with non-rewilding situations, 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 on system variable categories, while 195 observations from 32 primary studies were used to analyze the effect of specific biodiversity rewilding interventions on resilience, as studies addressing such were particularly frequent (see Results section). 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.

Second, to investigate how the type of disturbance, rewilding interventions, system variables, and resilience approach influenced the directional effects of rewilding on ecosystem resilience, we performed classification tree analyses (CTA). By examining class proportions for each rewilding component alone, we could identify which predictor variables were most relevant in determining the overall probability of positive, negative, or neutral resilience outcomes (Therneau et al., 2015). 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).

2.4.2. 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 (Supplement 3). 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).

3. Results

3.1. 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. 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/

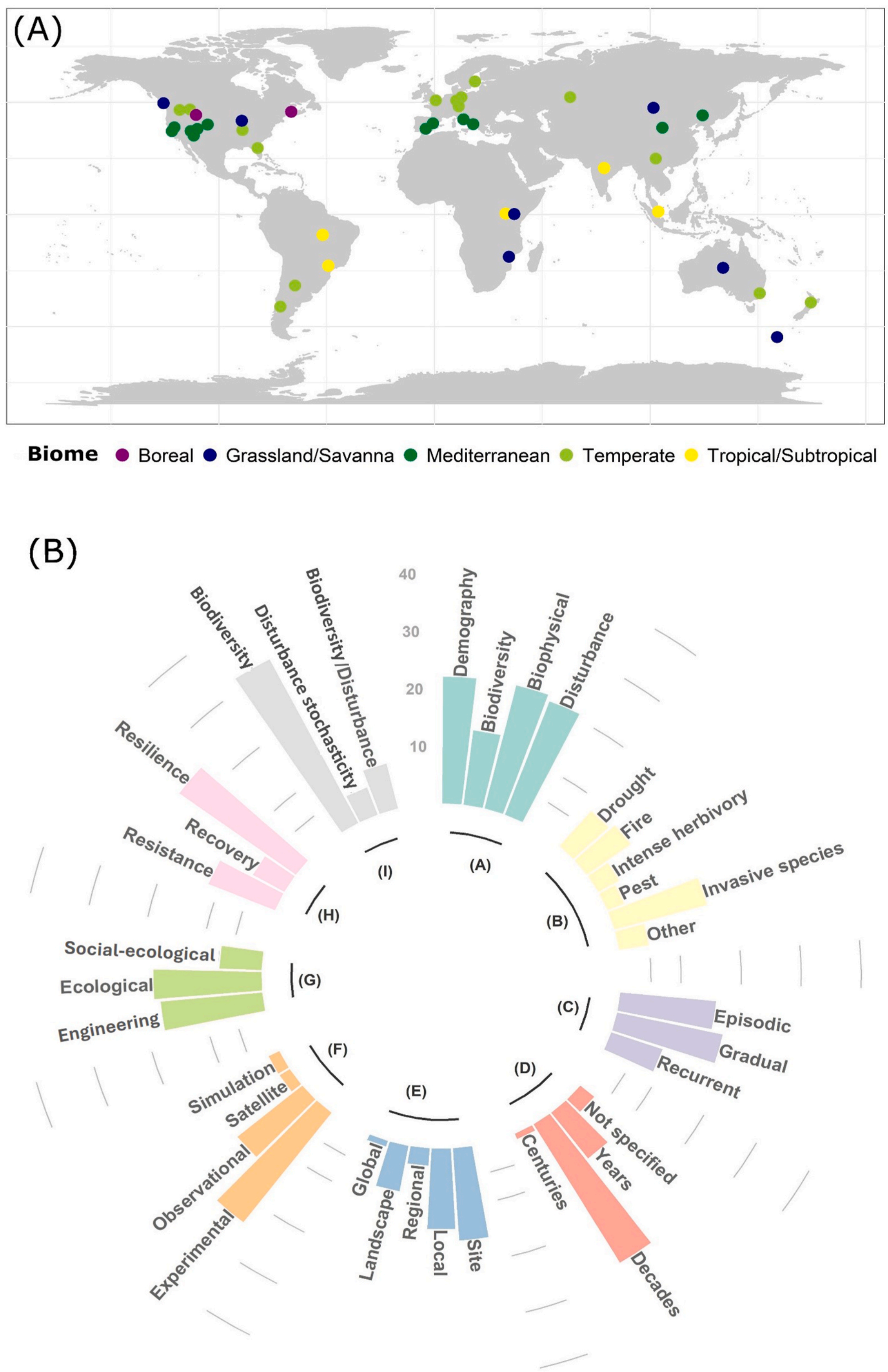

Fig. 2. (A) Geographic distribution of the 42 primary studies selected. Each point indicates a study location, and colors illustrate biomes using the global Köppen-Geiger climate classification. (B) Distribution of the Operational Resilience Framework (ORF) elements: A: system variable categories; B: 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 Supplement 2 for the complete list of variable descriptions.

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. 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. 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. 2B).

3.2. Directional effects of rewilding on resilience (vote counting and classification tree analysis)

Overall, 68.2% of the observations included in the vote counting analysis reported a positive effect of rewilding for increasing 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. 3A, Supplement 4). The benefits of rewilding to increase resilience after disturbances were observed for all four categories of system variables: demography, biodiversity, biophysical characteristics, and disturbance characteristics (Fig. 3B; Supplement 4). 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. 3C; Supplement 4).

In the same lines as the vote counting approach, the classification tree analysis also reported predominantly positive effects of rewilding for resilience (overall probability of positive resilience outcome = 72%, 45% and 79% for the biodiversity, disturbance and biodiversity/disturbance rewilding components, respectively; Supplement 5). Generally, for all rewilding components checked, the variables that showed major importance for positive resilience outcomes involved biotic disturbances, ecological resilience approaches, biodiversity system variables and prescribed fire and plant introductions (Supplement 5). As for the fewer cases when neutral or negative effects of rewilding on resilience where reported this included mostly the introduction or removal of animals or plants and other specific actions depending on the rewilding component. Regarding the biodiversity rewilding component, negative effects encountered mostly corresponded to abiotic disturbances, demography and disturbance system variables and plant introduction and removals (Supplement 5A). For the disturbance rewilding component, rewilding interventions that consisted of plant removals showed mostly neutral effects for resilience (Supplement 5B). And finally, for the biodiversity/disturbance component, animal introduction and plant removal rewilding interventions in the face of biotic disturbances showed negative effects for resilience (Supplement 5C). See Supplement B for specific positive, negative and neutral effects of each system variable assessed for each case study.

3.3. Effect size and effect of moderators (meta-analysis)

The overall effect of all three rewilding components on resilience was positive and significant (Fig. 4; Supplement 6) but showed high heterogeneity among observations ($Q_{Total} = 8813.62$, df = 279, $P < 0.001$). This latter 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; Supplement 6). Regarding resilience approach and dimension, rewilding was positive and significant for engineering and ecological resilience but showed non-significant effects for social-ecological resilience (Fig. 4; Supplement 6). Rewilding had a positive and significant effect when addressing resistance and recovery together (i.e., complete resilience dimension)

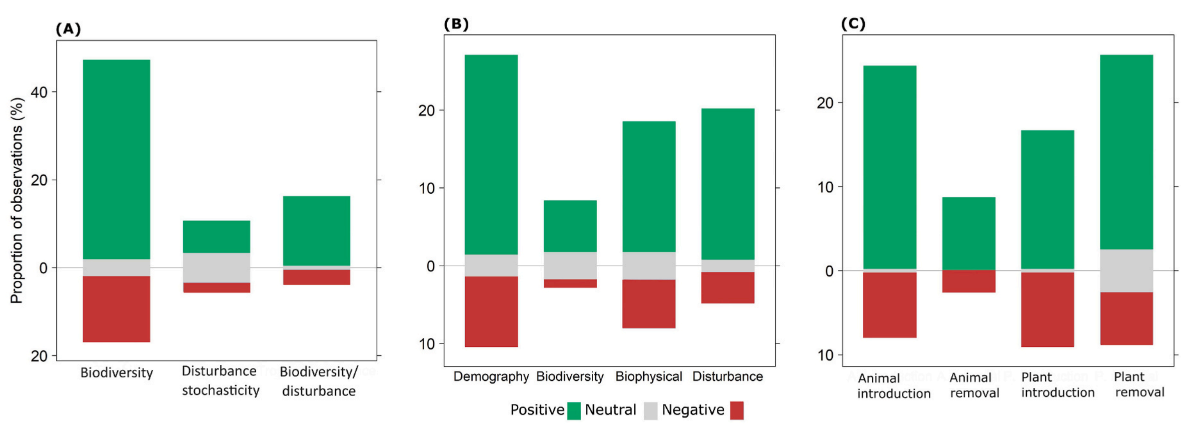

Fig. 3. Proportion of observations showing the direction effect (positive, neutral or negative) of (A) rewilding components for ecosystem resilience ($n_{observations} = 305$, $n_{primary\ studies} = 42$), (B) system variable categories for which resilience was assessed ($n_{observations} = 305$, $n_{primary\ studies} = 42$), and (C) specific rewilding interventions aimed at increasing biodiversity ($n_{observations} = 190$, $n_{primary\ studies} = 26$). n is the number of observations and primary studies considered. Note that the proportion of observations represented in each of the bars is not cumulative, but the sum of all bars in each figure sums up to 100%.

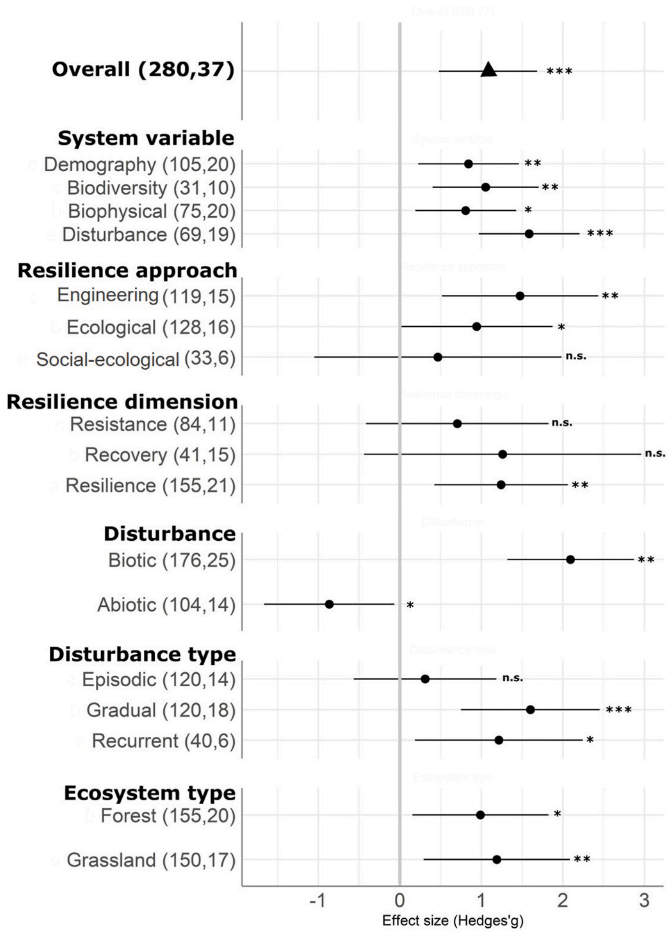

Fig. 4. Overall effect size (black triangle) and effect size for each group of moderators (black dots) together with their confidence intervals considering all rewilding components together (biodiversity, disturbance stochasticity, and biodiversity/disturbance). Effect sizes were calculated using Hedges'g. 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 Supplement 6 for the percentage of variation due to heterogeneity (I^2) and the heterogeneity among moderators (Q_M)).

while showing non-significant effects when considering the two components alone and separated (Fig. 4; Supplement 6). 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; Supplement 6). 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; Supplement 6). Finally, rewilding had significant positive effects on the resilience of both forests and grasslands (Fig. 4; Supplement 6).

Overall effect sizes for biodiversity, disturbance stochasticity and biodiversity/disturbance rewilding components were positive and significant (Fig. 5; Supplement 7) and showed high heterogeneity among observations. In addition, the meta-analysis was robust as indicated by the high Rosenthal's fail-safe number ($fsn_{Trophic}$ = 81,581, $fsn_{Disturbance}$ = 15,366, $fsn_{Trophic/Disturbance}$ = 15,503) showed a high value and therefore indicated robustness in meta-analysis. When considering each of the different rewilding components alone (Fig. 5; Supplement 7), 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. 5A), demography for the disturbance stochasticity rewilding component (Fig. 5B), and biophysical characteristics for the disturbance and biodiversity/disturbance components (Fig. 5B and C).

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. 6; Supplement 8). 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. 6, Supplement 8).

4. Discussion

We found predominantly positive outcomes (ca. 70 % of observations) 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 associated changes in disturbance regimes (Carroll and 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 (ca. 10%) or even fail (20%). According to our results, rewilding interventions exhibited lower resilience to abiotic disturbances such as drought. 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

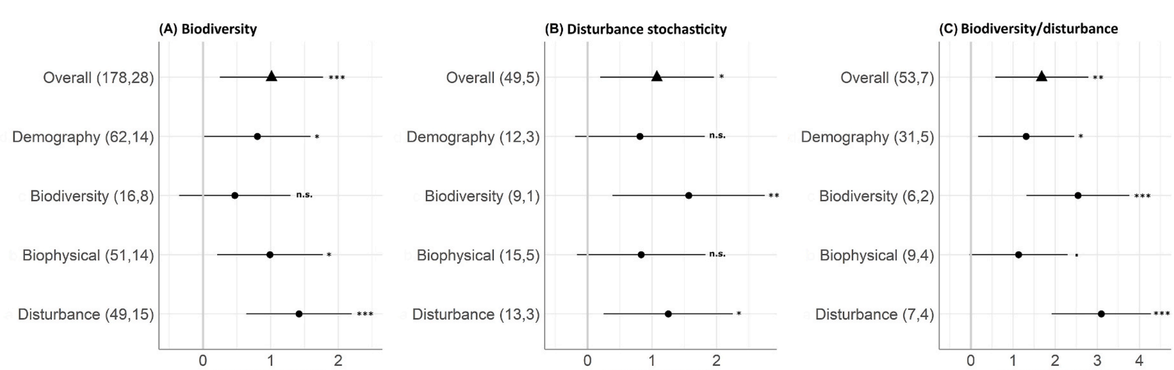

Fig. 5. Overall effect size (black triangle) and effect size for each system variable category (black dots) and their confidence intervals for (A) biodiversity, (B) disturbance stochasticity, and (C) biodiversity/disturbance rewilding components. Effect sizes were calculated using Hedges'g. Numbers in 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 Supplement 7 for the percentage of variation due to heterogeneity (I^2), and heterogeneity among moderators (Q_M).

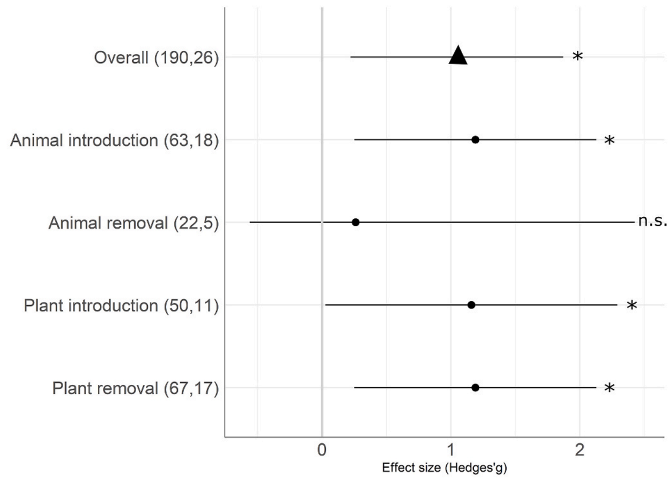

Fig. 6. Overall effect size (black triangle) and effect size for each specific biodiversity rewilding intervention (black dots) and their confidence intervals. Effect sizes were calculated using Hedges' g. Numbers in parentheses indicate the total number of observations and primary studies, respectively. Significant values are indicated by * (<0.05) and n. s. (non-significant). See Supplement 8 for the percentage of variation due to heterogeneity (I^2), and heterogeneity among moderators (Q_M).

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.

While our results, derived from a meta-analysis based on a conservative selection of articles that include both observational and experimental data, provide valuable insights, they should be interpreted with caution as although the number of studies scrutinized was very high (879) the number of studies that accomplished all the conditions for our analysis was relatively limited (42). Moreover, despite many of the studies relied on data collected decades after rewilding initiatives were implemented, only four case studies in our dataset accounted for the time elapsed since the disturbance event. This constraint limits our ability to robustly evaluate dynamic trends of resilience. Thus, future research should prioritize incorporating long-term temporal data and repeated measures over time, which would enable a more comprehensive understanding of resilience as a dynamic process.

Notwithstanding the growing attention towards rewilding 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 and 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 classification tree analysis and meta-analytical approach (Figs. 3 and 4; Supplement 5). 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). Interestingly, the highest proportion of neutral outcomes was observed for the disturbance rewilding component and was primarily linked to interventions involving plant removals (Supplement 5B), as illustrated by examples from the literature assessed. For example, Shackelford et al. (2019) observed that removing invasive species such as Scotch broom (*Cytisus scoparius*), Himalayan blackberry (*Rubus armeniacus*), and laurel-leaved daphne (*Daphne laureola*) had a neutral effect on the resilience of this grassland ecosystem to further invasions and native woody encroachment, leading to wildfire risk. In a similar way, Stephens et al. (2024) also found that mechanical plant removal did not show resilience benefits regarding future wildfire risk. Conversely, our results suggest that applying prescribed burning, rather than plant removal, as a restoration measure can be more effective to reduce wildfire vulnerability across various ecosystems (Supplement 5B). 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. 3). Specifically, the classification tree analysis for this component (Supplement 5A) revealed that case studies reporting negative effects on resilience were primarily linked to abiotic disturbances. These effects were most pronounced for system variables related to demography, as well as rewilding actions involving plant introductions and removals (Supplement 5A). Examples from the literature assessed such as Alba et al. (2024) reported that removing the invasive grass *Bromus tectorum* (cheatgrass) not only failed to enhance resilience to fire but also reduced the composition of native species. Similarly, Blumroeder et al. (2022) observed that removing non-native trees and introducing native ones did not lead to ecosystem resilience under future drought events. These cases highlight a notable failure of rewilding efforts to enhance resilience to abiotic disturbances such as fire and drought (Fig. 4) 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. 3B–Supplement 5A) 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), 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 (e.g., 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 social-ecological resilience (Fig. 4). This might be because social-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. Similarly, when analyzing resilience dimensions, the lack of significant effects for resistance and recovery when assessed separately contrast with the positive effects observed when they are combined (i.e., resilience) (Fig. 4). This suggests that the benefits of rewilding are more evident when resilience is evaluated as an holistic attribute rather than through its individual components. 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 category was almost universally enhanced by rewilding (Fig. 3B). A large amount of these positive biodiversity observations in the vote counting analysis (Fig. 3B) were mostly linked to the biodiversity rewilding component, particularly through interventions like wild or domestic herbivore introductions or invasive plant removal which effectively mitigated 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, ultimately enhancing biodiversity resilience (e.g., 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, we identified two case studies reporting negative effects on grassland resilience to invasive species (Assis et al., 2021; Cava et al., 2018), which led to contrasting results for the biodiversity system variable when examining the biodiversity rewilding component, as these effects were not significant (Fig. 5). This underscores, once again, the context-dependent nature of restoration practice outcomes. 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. 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).

5. 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.

CRediT authorship contribution statement

Miriam Selwyn: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alba Lázaro-González:** Writing – review & editing, Validation, Methodology, Data curation, Conceptualization. **Francisco Lloret:** Writing – review & editing, Validation, Conceptualization. **José María Rey Benayas:** Writing – review & editing, Validation, Conceptualization. **Arndt Hampe:** Writing – review & editing, Validation, Conceptualization. **Lluís Brotons:** Writing – review & editing, Validation, Conceptualization. **Joan Pino:** Writing – review & editing, Validation, Conceptualization. **Josep Maria Espelta:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.124360.

Data availability

The supplementary materials contains the articles used in this research, along with the key extracted data.

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