

No general support for functional diversity enhancing resilience across terrestrial plant communities

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Abstract

Aim: Understanding the mechanisms promoting resilience in plant communities is crucial in times of increasing disturbance and global environmental change. Here, we present the first meta-analysis evaluating the relationship between functional diversity and resilience of plant communities. Specifically, we tested whether the resilience of plant communities is positively correlated with interspecific trait variation (following the niche complementarity hypothesis) and the dominance of acquisitive and small-size species (following the mass ratio hypothesis), and for the context-dependent effects of ecological and methodological differences across studies.

Location: Global.

Time Period: 2004–2021.

Major Taxa Studied: Vascular plants.

Methods: We compiled a dataset of 69 independent sites from 26 studies that have quantified resilience. For each site, we calculated functional diversity indices based on the floristic composition and functional traits of the plant community (obtained from the TRY database) which we correlated with resilience of biomass and floristic composition. After transforming correlation coefficients to Fisher's Z-scores, we conducted a hierarchical meta-analysis, using a multilevel random-effects model that accounted for the non-independence of multiple effect sizes and the effects of ecological and methodological moderators.

For affiliations refer to page 13.

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Results: In general, we found no positive functional diversity–resilience relationships of grand mean effect sizes. In contrast to our expectations, we encountered a negative relationship between resilience and trait variety, especially in woody ecosystems, whereas there was a positive relationship between resilience and the dominance of acquisitive species in herbaceous ecosystems. Finally, the functional diversity–resilience relationships were strongly affected by both ecological (biome and disturbance properties) and methodological (temporal scale, study design and resilience metric) characteristics.

Main Conclusions: We rejected our hypothesis of a general positive functional diversity–resilience relationship. In addition to strong context dependency, we propose that idiosyncratic effects of single resident species present in the communities before the disturbances and biological legacies could play major roles in the resilience of terrestrial plant communities.

KEY WORDS

disturbance, functional diversity, mass ratio hypothesis, meta-analysis, niche complementarity hypothesis, resilience, terrestrial plant communities

1 | INTRODUCTION

Ecosystems around the world are changing at an unprecedented pace due to different human-induced drivers (e.g. land use and climate change) with important repercussions for diversity and ecosystem processes (Díaz, 2019; Jaureguiberry et al., 2022; Lee et al., 2023). Given the magnitude and speed of this change, it is crucial to better understand the processes that maintain ecosystem stability. Stability has two main components: resilience—the capacity of a system to recover from disturbances and maintain its functioning over time (stability in Holling, 1973, and engineering resilience in Holling, 1996)—and resistance—the capacity of a system to avoid change (Lepš et al., 1982). While the concept of resilience has become increasingly popular within the realms of both ecology and interdisciplinary science (Capdevila et al., 2021; Carpenter et al., 2001), our understanding of the components or mechanisms that underpin the resilience of ecosystems in the face of different drivers of change remains limited to specific spatial scales and ecosystems (Ives & Carpenter, 2007; Jentsch & White, 2019).

Resilience can be influenced by a number of sources of resilience (Lipoma et al., 2020), including both community properties, such as the number of resident species and their functional traits, and biological legacies, that is, organisms or structures remaining in the system after disturbance, such as soil seed and bud banks or surviving individuals (Klimešová et al., 2016; Oliver et al., 2015; Willis et al., 2018).

Much of the literature has concentrated on the positive effects of species richness on the resilience, or stability, of biomass production (Ives & Carpenter, 2007; McNaughton, 1977; Tilman et al., 2006; Tilman & Downing, 1994). The *insurance hypothesis of biodiversity* (Yachi & Loreau, 1999) posits that both resistance and resilience increase with increasing species richness. The basic

explanation is that if the various species in a community respond differently to environmental changes, then the decrease in one species in the community may be compensated by the increase in another species. Different mechanisms have been proposed to explain this variation in species responses (also response diversity, Elmquist et al., 2003), including dissimilar responses of species to environmental fluctuation (de Mazancourt et al., 2013) or interspecific trade-offs in competitive abilities (Tilman, 1999). Empirical support for these mechanisms has been mixed, with studies showing positive (Carvalho et al., 2013; Spears et al., 2015; Van Ruijven & Berendse, 2010), negative (Isbell et al., 2015) and non-significant (Fischer et al., 2016; Isbell et al., 2015; Wagg et al., 2017) effects of species richness on resilience, which casts doubts about the generality of this positive relationship.

In the attempt to understand the mechanisms in addition to focusing exclusively on the number of species, the functional trait approach integrates phenotypic characteristics with local abundance of species as determinants of ecosystem resilience (Díaz et al., 2007). There is a strong expectation that resilience is linked to the ecosystem's functional diversity, that is, the kind, ranges and relative abundances of functional traits present in a given community (Violle et al., 2007). However, only a few studies could ascertain clear links between functional diversity and resilience (hereafter functional diversity–resilience relationships). Even less is known about the environmental contexts that promote such links. The *niche complementarity hypothesis* (McNaughton, 1977; Tilman, 1999; Tilman & Downing, 1994) proposes one mechanistic explanation for the functional diversity–resilience relationships, positing that resilience depends on niche partitioning of species in the community. A wide variety of trait values (also trait range or trait differences, Díaz et al., 2007) can increase the chances that species present in the community possess particular trait combinations that enhance

survival following perturbations and compensate for the loss of other species, and thus, maintain or recover the overall 'functioning' of the ecosystem, resulting in resistance and resilience, respectively (Walker et al., 1999). Thus, a strong link would be expected between the insurance effect of biodiversity and the diversity of ecologically relevant functional traits in the community. The effect of higher trait variety was found to be positively related to resilience in communities recovering from biomass and topsoil removal (Schäfer et al., 2019), but unrelated in communities recovering from a flood (Fischer et al., 2016). It is important to mention that species richness has been used widely in the literature as a proxy of trait variation, especially when the full range of life-history strategies presented in a community cannot be fully represented by the functional trait data available (Biggs et al., 2020; Craven et al., 2018).

Additionally, the *mass ratio hypothesis* states that functional trait values of dominant species, that is, those with higher relative abundances, overwhelmingly shape the functional characteristics of the community, and thus drive many community properties, including resilience (Grime, 1998; Lepš et al., 1982). Specifically, trait values related to the resource-use strategies (acquisitive vs. conservative species) and to plant structure (big-size vs. small-size species), which are both related to a fast-slow growth gradient, are asserted to be related to resilience (Lepš et al., 1982; Macgillivray & Grime, 1995). Experimental studies that tested this hypothesis found that communities dominated by acquisitive species recovered faster from disturbances, such as fire, drought or mowing than communities dominated by conservative species (Macgillivray & Grime, 1995; Manninen & Tolvanen, 2013; Ruppert et al., 2015; Wardle & Jonsson, 2014).

The uncertainties regarding the functional diversity–resilience relationships may be affected by different ecological contexts, such as the disturbance regime (Jentsch & White, 2019) or the type of ecosystem and the variable studied (Bernhardt-Römermann et al., 2011; Hillebrand & Kunze, 2020). Schäfer et al. (2019) evaluated the functional diversity–resilience relationships following anthropogenic disturbances and observed a positive effect of functional richness (the trait space occupied by species in a community) on the resilience of plant cover, but no effect on the number of species present in the community. Similarly, Lipoma et al. (2016) evaluated the effect of the dominance of fast-growing species and found no effect on the resilience of total community cover, but a negative effect on the resilience of floristic composition after fire, indicating that functional diversity can have different effects on the resilience of structural variables (biomass and cover) than to the resilience of compositional variables (richness and species identity). Functional diversity–resilience relationships can also be affected by the intensity and duration of disturbances. When a disturbance has a low intensity and/or short duration, it may retain many biological legacies that increase the resilience of the ecosystem. After a high-intensity or long-lasting disturbance, instead, biological legacies may be less likely to play a major role (Allison, 2004; Belote et al., 2012; Lipoma et al., 2021). Differences in the lifespan and life-history strategies between species typical of woody or herbaceous ecosystems could also result in different functional diversity–resilience relationships.

The dominance of fast-growing and short-lived species can, for instance, increase resilience after disturbance in herbaceous ecosystems. Yet, woody ecosystems, dominated by long-lived, slow-growing species, can show a negative relationship between fast-growing plant dominance and resilience if they recover mainly from underground organs (Bernhardt-Römermann et al., 2011; Lipoma et al., 2016).

Methodological differences in experimental studies may obscure the true direction and shape of the functional diversity–resilience relationship, as studies vary in their design, length or the metrics used to evaluate resilience (Box 1, Ingrisch & Bahn, 2018; Isbell et al., 2015; Spake et al., 2021; Van Meerbeek et al., 2021). Moreover, most studies have evaluated functional diversity–resilience relationships at local spatial grains and extents. Consequently, we lack a synthetic perspective of the general effects of functional diversity on resilience across ecosystems.

In order to deepen our current understanding of functional diversity–resilience relationships, we analysed how the different components of functional diversity are related to the resilience of plant communities. We performed a meta-analysis of studies that quantitatively evaluated the resilience of different terrestrial plant communities, using systematic and reproducible quantitative methods to combine study results across multiple sites (Koricheva & Gurevitch, 2014).

We hypothesized that the resilience of plant communities is positively correlated with interspecific trait variation (following the niche complementarity hypothesis) and the dominance of acquisitive and small-size species (following the mass ratio hypothesis). However, we expect results to be context dependent, and therefore tested how functional diversity–resilience relationships would vary across:

1. plant community properties studied (specifically comparing variables related to biomass with those related to floristic composition),
2. biome or ecosystem type of the investigated community,
3. type, intensity and duration of disturbance events,
4. methodological study characteristics (such as the resilience metric, study design or length).

2 | DATA AND METHODS

2.1 | Literature search

In November 2021, we conducted a systematic literature search in Scopus and Web of Science repositories, focusing on published peer-reviewed studies that measured resilience in plant communities. In order to be included, a study had to meet the following criteria: (1) present primary data on terrestrial plant communities; (2) quantitatively evaluate resilience through the monitoring of plant communities after a disturbance rather than using space-for-time substitutions; (3) evaluate the resilience of biomass or floristic composition; (4) have a clear reference system; and (5) do not conduct

BOX 1

To promote comparisons across studies, Ingrisch and Bahn (2018) classified the resilience metrics in three categories that differ fundamentally depending on the component of resilience they address. Here categories are described and one example equation is presented for each.

Category I (Normalized system state) comprises metrics describing the impact of a disturbance on a response variable in relation to the reference. Because these metrics do not include a disturbed state, the resilience cannot be completely disentangled from resistance.

$$\text{Resilience} = \frac{\text{Recovered state}}{\text{Reference}}$$

Category II (Baseline-normalized recovery) focuses primary on the change between the disturbed state and the recovery state.

$$\text{Resilience} = \frac{(\text{Recovered state} - \text{Disturbed state})}{\text{Reference}}$$

Category III (Impact-normalized recovery) focuses on the recovery relative to the disturbance impact. These metrics include the amount of change between the reference and the disturbed state and also between the recovered and the reference states.

$$\text{Resilience} = \frac{(\text{Disturbed state} - \text{Reference})}{(\text{Recovered state} - \text{Reference})}$$

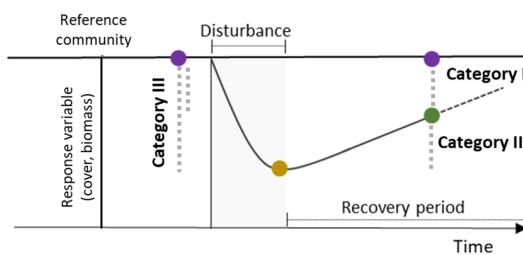
Resilience Categories

Figure 1. The response of an arbitrary variable (for instance vegetation cover or biomass) to a disturbance (grey area) and its change over time and how different categories of resilience metric are assessed. Points represent different states of the system in time: violet points represents the reference state, yellow represents the disturbed state (during or immediately after the disturbance), and green represents the system under a recovery path. Dashed lines represent differences in the response variable between different system states and the different categories are shown next to the differences each of them used for calculating resilience. See that category III uses both the difference between the recovered state and the reference state and the difference between the reference state and the disturbed state to calculate resilience.

any active restoration or reclamation practice. The complete search string and the specific inclusion criteria are listed in Appendix S1.

After the removal of duplicates, the systematic search returned 5303 studies. The screening of the titles and abstracts led us to exclude the vast majority of studies (4706). We examined the full text of the remaining 597 papers, 78 of which qualified based on our selection criteria. Additionally, we added four studies from our personal database (Fischer et al., 2016; Kreyling et al., 2017; Lanta et al., 2012; Lepš et al., 1982) that met our inclusion criteria but were not detected in the systematic search, yielding a total of 82 selected studies.

Due to the low number of studies presenting any correlation between resilience and functional diversity, we decided to use primary data from each study to calculate the correlation value ourselves. When the needed information was not extractable from the information published, we contacted authors and asked them to share raw values of resilience and pre-disturbance floristic composition (species identity and abundance values defined within each study) for each vegetation plot in the study. In some cases, we used these primary data to calculate the resilience index using the same index described in the respective study (Appendix S2). Floristic composition data were necessary to calculate functional diversity indices (see below). This resulted in a final set of 26 studies that were included in the analysis, covering 69 independent sites with a total of 8181 individual plot observations mainly distributed not only across Europe but also across North and South America (Figure 1, Appendix S2).

2.2 | Database compilation

The database comprised vegetation data containing two data subsets, one with total number of species (69 sites) and the other with

species identity and abundance (48 from 69 sites). We combined the subset containing identity and abundance with functional traits data from the TRY database 5.0 (Kattge et al., 2011). We used species-specific values of 19 functional traits which describe different strategies that are expected to be related to species' responses to disturbances (Appendix S3). A gap-filling method was applied to this data as was done in Bruelheide (2018) (see Appendix S3 for details about the gap-filling method). The gap-filled trait database contained data for 61% of the species included in the analysis, although this percentage was not the same for all sites, ranging from 95% to 5.8%. Sites with fewer than 50% of species with trait data (corresponding also to sites where trait data were available for species cumulatively accounting for <60% of the biomass) were excluded from the calculations of functional diversity indices and only the value of species richness for these sites was used. We conducted the same analysis using a shorter but more extensively measured list of traits used for the global spectrum of form and function (Díaz et al., 2015), obtaining very similar results despite not increasing the number of records used in the analysis (Appendix S7).

Additionally, we extracted information from each study on ecological and methodological characteristics that we expected to moderate the observed functional diversity–resilience relationships (hereafter moderators, Table 1). One important difference between studies was the metric used to evaluate resilience. We classified the different resilience metrics according to the categories proposed by Ingrisch and Bahn (2018) (Box 1). We only included studies that used metrics from categories I and III because they were the most commonly used, and because studies that included a metric from category II also included another metric from category I or III. By including category as moderator, we could analyse together studies that used different metrics to evaluate the response of plant



FIGURE 1 Location of sites where functional diversity-resilience relationships were evaluated. Total number of sites $n=69$. Please note that some points are close to each other and may appear as single points.

communities to disturbances and account for the possible effect of the choice of the metrics.

2.3 | Data preparation

2.3.1 | Calculation of functional diversity indices

Using species identity, abundance and functional trait data collected for each site, the following multi-trait indices were calculated to quantify the functional diversity of plant communities in each study: species richness (SR), functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), functional evenness (FEve) and community-weighted means representing life-history strategies (CWM) (Table 2 and Appendix S3). Index selection was based on those that are well supported by the literature (Table 2) and that show low correlation values between them (Appendix S3). For calculating CWMs, instead of individual CWM values for each trait, we summarized the community-weighted mean values of multiple traits (an indicator for the dominance of certain trait syndromes) by using their CWM scores along the first two axes of a principal component analysis (PCA) across all species (see Appendix S3 for details about the PCA analysis). The first principal component accounted for 23.7% of CWM variation and was negatively correlated with

traits representing plant structure and size: plant height, seed mass, leaf dry mass and leaf area and was indicated as a 'small-plant dominance' axis. The second principal component accounted for 14.9% of CWM variation and was positively correlated with traits related mainly to resource acquisition: specific leaf area and leaf phosphorus and nitrogen concentration, and was indicated as an 'acquisitive dominance' axis. In this sense, both axes can be interpreted in the context of a fast-slow growth gradient (Wright et al., 2004) and are expected to show a positive correlation with resilience (Grime, 1977; Lepš et al., 1982).

2.3.2 | Calculation of effect size

For each study site, we calculated Pearson's correlation coefficients between resilience and the different functional diversity indices of the monitored vegetation plots. To achieve approximately normal distributions, we transformed all correlation coefficient values to Fisher's Z-scores (hereafter effect size, Equation (1), where r is Pearson's correlation coefficient) together with the respective measure of effect size variance (Equation (2), where N is the sample size). Fisher's Z-score is a common metric in meta-analysis which ranges from $-\infty$ to $+\infty$ and follows approximately a normal distribution (Koricheva & Gurevitch, 2014).

TABLE 1 Information of moderators extracted from each study.

Variable	Description	Categories/units
Ecological characteristics of studies		
1. Ecosystem type	The ecosystem types reported in each study were classified depending on the growth form of plants that are dominant	Woody and herbaceous ecosystems
2. Response variable	Response variables were either related to biomass or floristic composition	Biomass-related characteristics: total number of individuals, cover or biomass Floristic composition: richness and similarity indices
3. Biome	Following Olson et al. (2001)	Tropical and subtropical moist broadleaf forests (TrBF); tropical & subtropical dry broadleaf forests (TrF); tropical & subtropical coniferous forests (TrCF); temperate broadleaf & mixed forests (TBF); temperate conifer forests (TCF); boreal forests/taiga (BF); tropical & subtropical grasslands, savannas & shrublands (TrG); temperate grasslands, savannas & shrublands (TG); flooded grasslands & savannas (FIG); montane grasslands & shrublands (MGS); tundra (Tu); Mediterranean forests, woodlands & scrub (MF); deserts & xeric shrublands (DS); mangroves (Man)
4. Response component	Indicates if the response variable represents the complete community or a particular component (a particular group of plants)	Complete community, woody vegetation and understory vegetation
5. Disturbance type	According to the kind of disturbance. Disturbance was defined as any event characterized by directly altering biomass and ecosystem structure (sensu Grime et al., 1997; and mentioned as 'biomass-altering disturbances' in Jentsch & White, 2019)	Direct biomass removal (fire, herbivory, logging, mowing, soil disturbances, trampling, wind and flood) Wet climatic events (wet years) Dry climatic events (dry years)
6. Disturbance duration	How long has the disturbance affected the ecosystem?	Days
7. Disturbance intensity	As reported in each study	Low, medium and high
Methodological characteristics of studies		
8. Temporal scale	Period of monitoring after the disturbance	Days
9. Community origin	Distinguishes natural communities that were demarcated in the field from artificial communities that were assembled through seeding	Natural or artificial
10. Study design	Describes how the study evaluates the response of the community to disturbances	'Before and After studies' (BAS) compare the pre-disturbed condition with the post-disturbed condition 'Parallel studies' (PS), including a parallel control, when no pre-disturbance data are available 'Before and After/Control and Impact' (BACI), where comparisons include both a parallel control and a pre-disturbance control to incorporate changes due to climate variation
11. Study type	Distinguishes disturbances experimentally conducted from 'natural or unexpected' disturbances	Manipulative or observational
12. Plot size	Area of the observational unit	m^2
13. Resilience metric category	Following Ingrisch and Bahn (2018)	I, II and III (See Box 1 for a detailed explanation)

$$Z = \frac{1}{2} \ln \left(\frac{1+r}{1-r} \right) \quad (1) \quad 2.3.3 \mid \text{Data preparation of moderators}$$

$$\text{Var}_z = \frac{1}{N-3} \quad (2) \quad \text{Moderator variables were not completely independent in our datasets. For instance, disturbances related to dry or wet climatic}$$

TABLE 2 Detailed description of the different functional diversity indices used and the references for each one.

Index		Description	Formula
Species richness	SR	Number of species	
Functional richness (Villéger et al., 2008)	FRic	The volume of the multidimensional trait space occupied by all species in a community. It does not include species abundances	Quickhull algorithm
Functional dispersion (Laliberte & Legendre, 2010)	FDis	The mean distance in multidimensional trait space of individual species to the centroid of all species weighted by their abundances	$c = \frac{\sum a_j x_{ij}}{\sum a_j}$ $FDis = \frac{\sum a_j z_{ij}}{\sum a_j}$ c, centroid of the trait multidimensional space of all species in the community weighted by the abundance of each species; a_j , abundance of species j ; x_{ij} , value of species j for trait i ; z_{ij} , distance of species j to the centroid c
Functional divergence (Villéger et al., 2008)	FDiv	The proportion of total abundance supported by species with the most extreme trait values within a community.	$FDiv = \frac{\Delta d + dG}{\Delta d + dG}$ dG, mean distance to the centroid of the trait multidimensional space of all species in the community; Δd , sum of abundance-weighted deviances from the centroid, $\Delta d $, absolute abundance-weighted deviances from the centroid
Functional evenness (Villéger et al., 2008)	FEve	The regularity of the distribution and relative abundance of species in the multidimensional trait space occupied by all species in a community	$EW_{ij} = \frac{d(i,j)}{w_i + w_j}$ $PEW_i = \frac{EW_i}{\sum_{i=1}^s EW_i}$ $FEve = \frac{\sum_{i=1}^{s-1} (PEW_i \cdot \frac{1}{s-1}) - \frac{1}{s-1}}{1 - \frac{1}{s-1}}$ EW, weighted evenness between two species; d_{ij} , functional distance between species i and j ; w_i and w_j , relative abundances of species i and j ; s , total species richness; PEW, partial weighted evenness
Community-weighted life-history strategies	Small-plant dominance axis and acquisitive dominance axis	The degree of dominance of fast-recovering species in the community	$CWM = \sum_{i=1}^s (x_i \cdot w_i)$ s, total species richness; x_i , the score of the species i in the correspondence PCA axis; w_i , the relative abundance of species i in the community

events were only studied in herbaceous ecosystems, and study length was generally longer for woody ecosystems. In order to account for this non-independence of moderators, we used principal coordinates analysis (PCoAs), based on Gower's dissimilarities, across all moderators to divide our datasets into studies with similar ecological and methodological study characteristics and delineate common axes of variation (see Appendixes S4 and S5, and Table 1 for a description of each moderator). By subdividing the datasets, the number of moderators and, as a consequence their correlation, were reduced.

According to the PCoAs, a major source of heterogeneity was related to ecosystem type, differentiating woody from herbaceous ecosystems. Additionally, studies from woody ecosystems evaluated the resilience of biomass and the resilience of floristic composition, while studies from herbaceous ecosystems evaluated mainly the resilience of biomass (just one study analysed the resilience of floristic composition). Accordingly, we divided the dataset into three subgroups: (1) herbaceous biomass: communities from herbaceous ecosystems where the resilience of biomass was studied, (2) woody biomass: communities from woody ecosystems where the resilience of biomass was studied and (3) woody composition: communities from woody ecosystems where the resilience of floristic composition was studied. For each data subgroup, remaining correlations

between moderators were synthesized using PCoA axes (see Appendixes S4 and S5 for a detailed description of the PCoAs).

2.3.4 | Statistical analysis

We conducted a series of separated random-effect meta-analyses to calculate the grand mean effect size (i.e. average Fisher's Z-scores) to test the prediction that resilience would be positively correlated with (1) a greater variation of trait values (using SR, FR, FDis, FDiv and FEve indices) and (2) the dominance of fast recovering species (using the small-plant dominance and acquisitive dominance axes). We included the research site as a random factor to account for the lack of independence between measurements at the same site. Grand mean effect sizes were considered to be statistically significant if the approximated 95% confidence intervals (CIs) did not include zero. In addition, we calculated the amount of residual heterogeneity (τ^2) and we visually inspected funnel plots between effect sizes and effect size variances.

We expanded each model by adding the axes of moderator variation as predictor variables. We used an omnibus test of moderators (QM) to test for the significance of the moderator axes in explaining the heterogeneity of effect sizes between independent sites.

Subgroup average effect sizes were considered statistically significant if the approximated 95% CIs did not include zero.

All statistical analyses were conducted in R (R Core Team, 2021) using the package 'metafor' for meta-analyses (Viechtbauer, 2010), the *dbFD* function of the 'FD' package for functional diversity indices calculations (Laliberté et al., 2014), 'stats' package for the PCA analysis, *capscale* function of the 'vegan' package for PCoA analysis (Oksanen et al., 2022) and 'ggplot2' (Wickham, 2009) for graphics.

3 | RESULTS

Across the full dataset, grand mean effect sizes for the effect of functional diversity on resilience were statistically non-significant, except for a negative correlation of resilience with functional dispersion (FDis), meaning that plant communities with trait values highly different from each other before a disturbance showed lower resilience (Figure 2).

All meta-analytical models displayed large amounts of unexplained heterogeneity, indicating the existence of differences in effect sizes across sites (Appendix S6).

Grand mean effect sizes remained mostly non-significant when we divided the dataset into subsets tackling separately: (1) the

resilience of biomass in herbaceous ecosystems, (2) the resilience of biomass in woody ecosystems and (3) the resilience of floristic composition in woody ecosystems. The only exceptions included a positive correlation between the resilience of biomass with the acquisitive dominance axis in herbaceous ecosystems and a negative correlation between resilience of biomass and FDis in woody ecosystems (Figure 3).

Variation in ecological and methodological study characteristics affected the functional diversity-resilience relationships both in herbaceous (Figure 4) and in woody (Figure 5) ecosystems. In herbaceous ecosystems, for which only the resilience of biomass-related characteristics was evaluated, the correlation between resilience and FDis changed from negative to positive depending on the biome analysed and on methodological characteristics such as the temporal scale and the study design (Figure 4a). The correlation between resilience and the dominance of small species was also affected by ecological variables, such as the type of community and the type and duration of the disturbance, and methodological variables, such as the study design and the resilience metric used (Figure 4b).

In woody ecosystems, the direction of the relationship between the resilience of biomass-related characteristics with either FDiv or the dominance of acquisitive species was affected by biome type, showing positive correlation values for communities from boreal

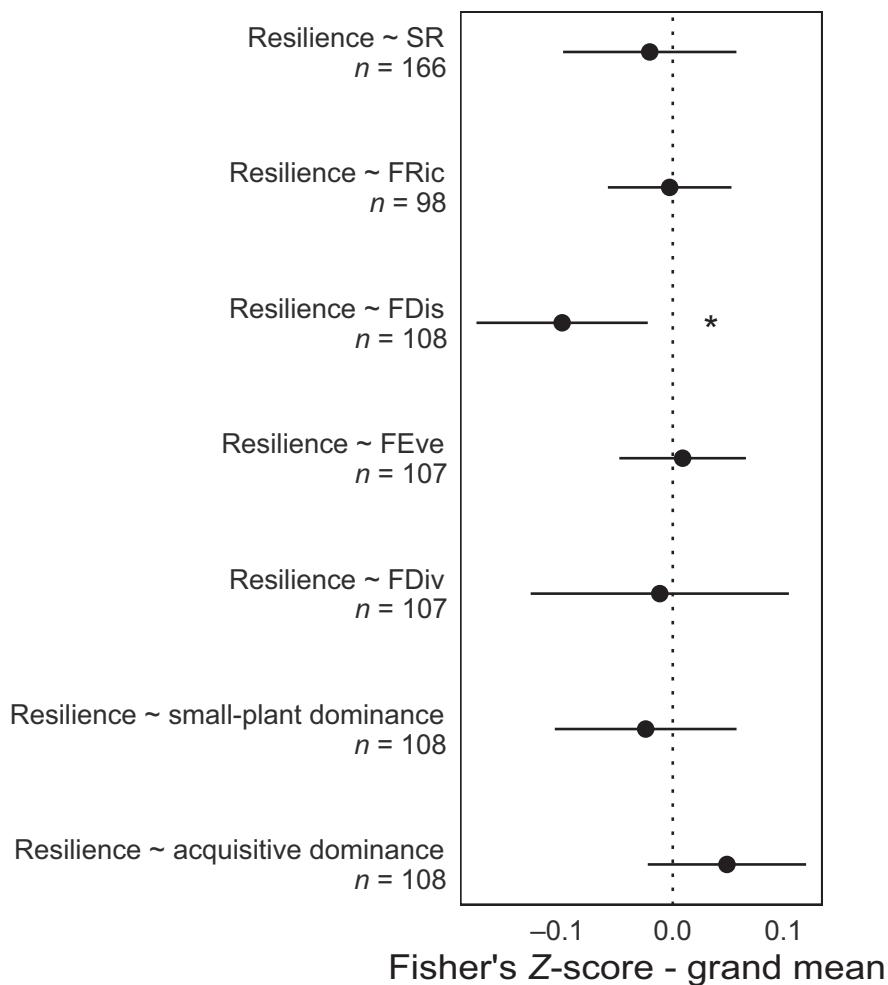
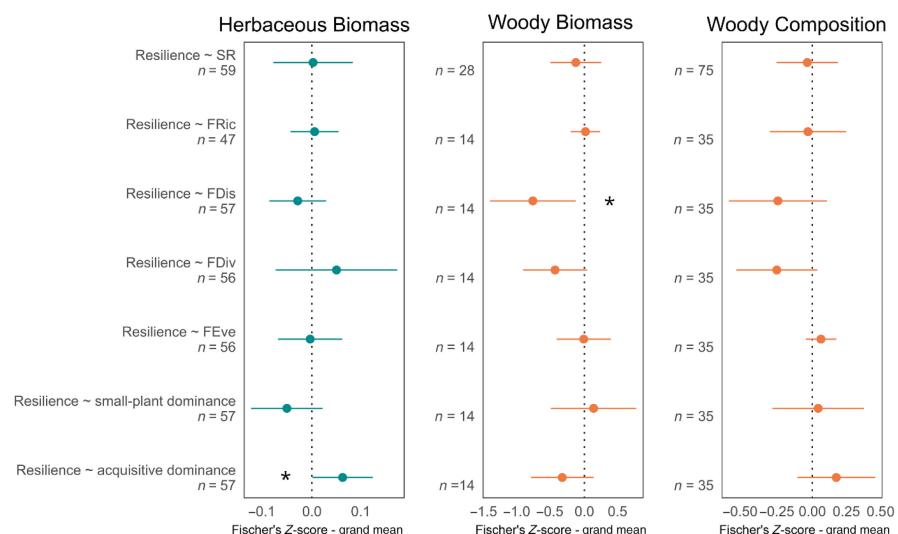
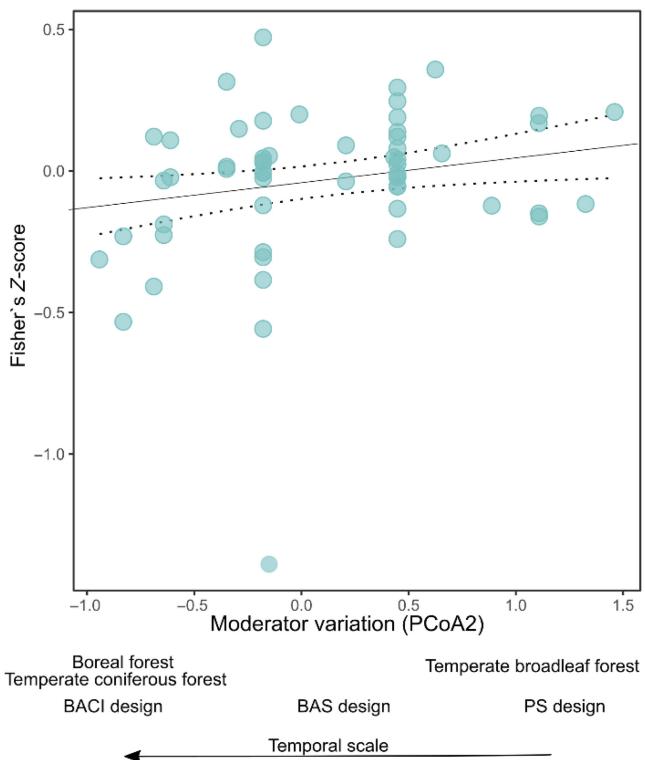


FIGURE 2 Grand mean-effect sizes of the different meta-analyses evaluating the correlation between resilience and different components of diversity. Species richness (SR), functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), functional evenness (FEve) and dominance of small and acquisitive species. Values for *n* indicate the total number of effect sizes for each analysis. **p* < 0.05.

FIGURE 3 Grand mean-effect sizes of meta-analyses evaluating the correlation between the resilience of biomass-related characteristics and the resilience of floristic composition with different components of diversity: species richness (SR), functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), functional evenness (FEve) and the dominance of small and acquisitive species in herbaceous (blue) and woody (orange) ecosystems. Values for n indicate the total number of effect sizes for each analysis. * $p < 0.05$.



(a) Herbaceous biomass ~ FDis



(b) Herbaceous biomass ~ Small-plant dominance

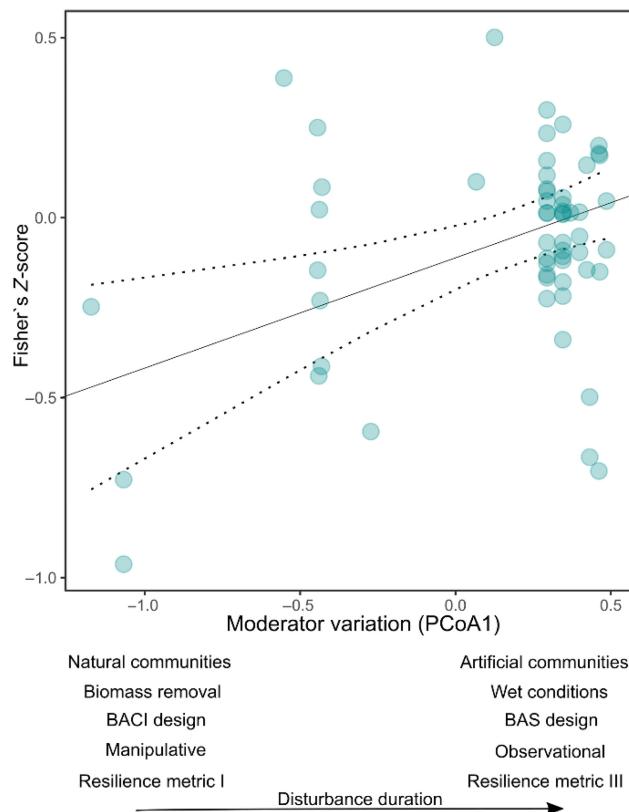


FIGURE 4 Relationship between the axes of moderator variation and the transformed correlation coefficients (Fisher's Z-scores) between (a) resilience of biomass and the functional dispersion (FDis) and (b) the dominance of small species in herbaceous ecosystems. Each point represents an effect size, the solid line indicates the regression slope and the dotted lines show the approximated credible interval in a mixed-effects meta-regression model. Moderator variation axes represent ecological and methodological variation between studies that were summarized by principal component analyses (PCoA) as described in [Appendices 4](#) and [5](#).

or Mediterranean forests and negative values for communities from temperate forests ([Figure 5a,b](#)). The correlation between the resilience of floristic composition and FRic or FDiv was positive

for studies with a longer temporal scale and located mainly in the temperate biomes, while studies with a shorter temporal scale and located mainly in the tundra biome showed negative correlations

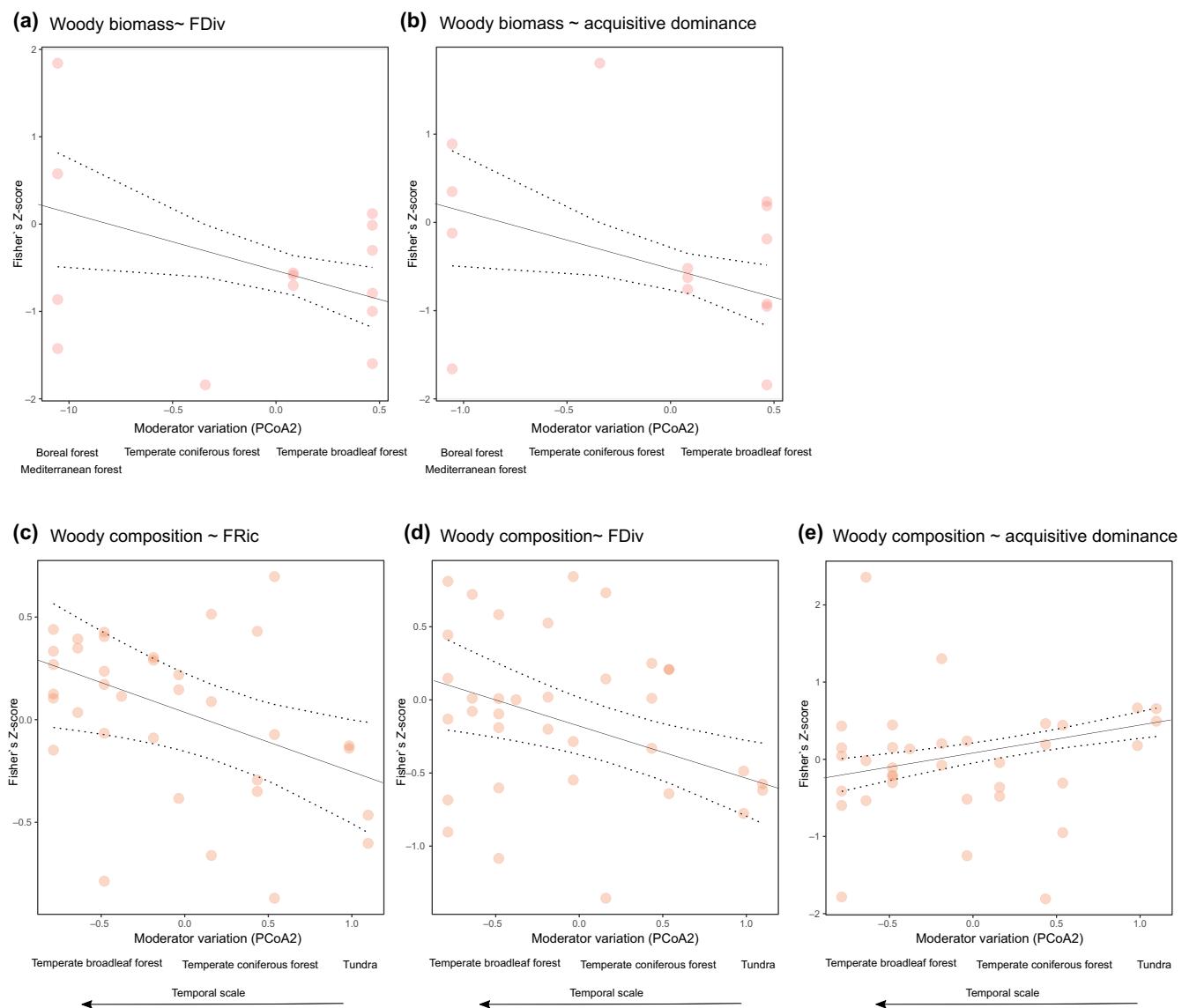


FIGURE 5 Relationship between the axes of moderator variation and the transformed correlation coefficients (Fisher's Z-scores) between (a) resilience of biomass and functional divergence (FDiv), (b) resilience of biomass and the dominance of acquisitive species, (c) resilience of floristic composition and functional richness (FRic), (d) resilience of floristic composition and functional divergence (FDiv) and (e) resilience floristic composition and the dominance of acquisitive species for communities from woody ecosystems. Each point represents an effect size, the solid line indicates the regression slope and the dotted lines are the corresponding approximated credible interval in a mixed-effects meta-regression model. Moderator variation axes represent ecological and methodological variation between studies that were summarized by principal component analyses (PCoA) as described in [Appendices 4](#) and [5](#). Please note that moderator variation axes are the same for figures a and b and figures c-e, but they differ between the two groups.

(Figure 5c). Finally, the correlation between the resilience of floristic composition and the dominance of acquisitive species showed the opposite trend from Fric or FDiv (Figure 5d).

4 | DISCUSSION

The present study represents the most comprehensive analysis to date of the relationship between resilience and functional diversity in terrestrial plant communities. Our results did not support the proposed

hypotheses of increasing resilience as a result of increased variety of functional traits or the dominance of acquisitive or small species. Instead, we found empirical support for the prediction that functional diversity-resilience relationships are affected by the ecological and methodological context. We delineate here three possible explanations for the absence of a general effect of functional diversity on resilience in terrestrial plant communities. Subsequently, we discuss the only two results indicating a functional diversity-resilience relationship different from zero, and finally, we present difficulties and recommendations for future studies.

4.1 | Possible explanations for an absence of a general effect of functional diversity on resilience

4.1.1 | Sources of resilience related to biological legacies

First, if functional diversity does not play a role, other sources of resilience may be involved. It is well supported in the literature that biological legacies, such as the presence of persistent seed, seedling or bud banks and the dispersion and colonization from undisturbed patches in the neighbourhood, influence resilience when the floristic composition of these legacies resembles that of the reference vegetation (Klimešová et al., 2016; Rudolphi et al., 2014). Although there are some general links between the persistence of these biological legacies and the functional traits present in the communities (e.g. recruitment limitations of some functional groups, Symstad & Tilman, 2001; seed size and persistence in the soil bank, Thompson et al., 1996), regeneration strategies are often considered to be relatively independent of resource-use syndromes (in the '*regeneration niche model*' of Grubb (1977) and as '*regeneration strategies*' by Grime (1977) and in the '*persistence niche model*' of Bond and Midgley (2001)). Additionally, other processes like secondary dispersion can be more dependent on vegetation structure or the presence of dispersal agents than on plant species functional traits (Lipoma et al., 2019). Nevertheless, there is still a long way to go until we understand how biological legacies and functional diversity together influence vegetation resilience.

4.1.2 | Species and trait idiosyncrasy

Second, other functional aspects different from trait variety or the dominance of fast-growing species may also be related to the resilience of plant communities after disturbances. Some studies have highlighted that the presence of particular species in the community can better explain resilience after disturbances than species or functional richness (Fischer et al., 2016; Speed et al., 2010; Van Ruijven & Berendse, 2010). This idiosyncratic effect of species that are not necessarily the most abundant (kind sensu Díaz et al., 2007; and identity sensu Symstad et al., 1998) on community resilience may not be associated with a generalizable set of functional traits, but rather with traits that determine a certain strategy in the face of a particular type of disturbance. In our study, herbaceous communities showed a positive relationship between resilience and the dominance of more acquisitive species, as was expected by our predictions, whereas woody communities did not. In the latter ecosystems, other traits (not related directly to resource acquisition or plant structure) may be relevant to resilience. For example, some studies have suggested that traits related to vegetative regeneration (that were not available for all species in our study) can explain recovery after disturbances in shrublands (Lipoma et al., 2016), savannas (Pilon et al., 2021) and in Mediterranean forests (Díaz-Delgado

et al., 2002). Other studies specifically point to the role of non-structural carbohydrates (D'Andrea et al., 2021; Martínez-Vilalta et al., 2016) or traits related to mutualistic association strategies (Jia et al., 2020) in communities subjected to climatic disturbances. However, except for some important efforts (Klimešová & Bello, 2009; Tavşanoğlu & Pausas, 2018), these traits have not been exhaustively studied (Larson & Funk, 2016) and may not be predictable from other measured traits (Mommer & Weemstra, 2012), hampering the analyses of their influence across ecosystems at a global level.

4.1.3 | Ecological and methodological context

Third, characteristics related to the ecological and methodological context of studies influenced the functional diversity–resilience relationships. This interpretation was partially supported by the impact of the main axes of moderator variation that summarized ecological and methodological characteristics that are not necessarily linked but rather reflect the current distinction in study types. The effect of these axes points to the key role of biome and temporal scale in mediating the relationship between functional diversity and resilience in woody ecosystems. Moreover, some disturbances (duration and type) and methodological characteristics of studies (study design, community origin and resilience metric) affected the relationship between functional diversity and resilience in herbaceous ecosystems. Regarding ecological characteristics, it has already been suggested that disturbance type and severity influence functional diversity–resilience relationships (De Boeck et al., 2018; Schäfer et al., 2019). In particular, positive effects were found mainly after short and mild disturbances, while after long-lasting or recurrent disturbances, the recovery may be less related to the characteristics of the pre-disturbance state than to those of the disturbed state (Burton et al., 2020; De Boeck et al., 2018; van Moorsel et al., 2021; Van Ruijven & Berendse, 2010). As a consequence, resident species may have been already filtered and may be adapted to the disturbance rather than to the pre-disturbance state, highlighting the importance of disturbance history for understanding the relationship between functional diversity and resilience. The effect of disturbances on the functional diversity–resilience relationship can also result in a lack of relationship if the disturbance has a between-plots homogenization effect and all plots recover (or not) from a community with a similar functional diversity, obscuring the functional diversity–resilience relationship if any. Specific analyses including the effect of disturbances on the assemblage of community (such as '*equalizing*' or '*stabilizing*' effect sensu Chesson, 2000) could help to understand the lack of functional diversity–resilience relationship.

One particular methodological aspect of resilience studies is that they are often restricted to the first months or years after disturbance, and if recovery is not achieved before the studies finish, they may fail to detect functional diversity–resilience relationships.

(Tilman et al., 2006). This might also explain the discrepancy between studies evaluating resilience and those evaluating resistance, a variable that can be measured right after the disturbance and that has been frequently associated with functional diversity (e.g. Bernhardt-Römermann et al., 2011; Fischer et al., 2016; Isbell et al., 2015). However, we currently lack enough temporal resolution and study duration to resolve these discrepancies.

4.2 | Detected functional diversity–resilience relationships

Instead of positive functional diversity–resilience relationships, there were some significant negative ones. A negative effect of the variation of functional traits on resilience was observed (represented by the functional dispersion index), especially in woody ecosystems, indicating that plant communities with a higher variety of trait values before the disturbance were less resilient, opposing the prediction of the niche complementarity hypothesis (Tilman & Downing, 1994), which means that in these communities, species with larger trait value differences may not complement each other after the disturbance, and species that survive may not contribute much to the resilience of the community. This might happen, for example, if species that exhibit the appropriate functional trait values to recolonize a site after a disturbance do not fully replace the biomass of the species that disappeared, resulting in incomplete recovery of the community in terms of biomass (Symstad & Tilman, 2001). The apparent lack of compensatory dynamics between species after disturbances may be also related to the recruitment limitation of survivors (Symstad & Tilman, 2001) or the disappearance of positive interactions between resident species after some of the species are lost (Butterfield, 2009; de Bello et al., 2021; Van Ruijven & Berendse, 2010). For example, there is evidence of higher vegetation recovery when nurse species are still present or recover quickly after the disturbance (Raffaele & Veblen, 1998; Speed et al., 2010). The fact that FDis index but no other indices showed significant results reinforces the fact that these indices represent different dimensions of the variation in trait values in communities (e.g. FDis considers the total trait space occupied by the species in the community, while FDiv only considers the proportion of abundance accounted by the most extreme species in the community and may remain unchanged if the total trait space is reduced without changing this proportion (Laliberte & Legendre, 2010; Villéger et al., 2008)). Additionally, differences between indices can be explained by the fact that FDis includes the cwm of all traits measured and their variation (see Table 2) and can show some degree of correlation with the dominance of specific traits, while the rest of the indices are completely independent (Appendix S3).

Finally, we found evidence of the positive effect of dominant traits on resilience (supporting the mass ratio hypothesis, Grime, 1998), although this only held for herbaceous ecosystems and the relationship between the resilience of biomass and the

dominance of functional traits related to resource-use acquisition (specific leaf area, phosphorus content, leaf area, specific root length and seed length). In these communities, the collective biomass of more acquisitive species recovered after disturbance, likely because of their fast resource acquisition rates (Lepš et al., 1982; Macgillivray & Grime, 1995).

4.3 | Caveats and recommendations for future empirical and meta-studies

Despite the high number of published studies evaluating resilience, the majority did not present an index of resilience that would allow them to be included in this meta-analysis. In total, we identified 160 studies that met almost all the inclusion criteria, except that they did not present an index of resilience. Instead, these studies presented the value of a response variable in time after disturbance or a comparison of means of the response variable between the recovery state and the control state. It would be important to consider including these studies in future analysis, which, however, requires their collection and re-analysis based on raw data. Additionally, we found that, although being frequently mentioned, the functional diversity–resilience relationships are not consistently evaluated in studies analysing the resilience of plant communities, an issue that we addressed by using data provided by authors to calculate correlation values. As a consequence, we also reduced potential biases resulting from the tendency to publish predominantly positive diversity–stability relationships.

We included studies that used different metrics of resilience (categories I and III according to Ingrisch & Bahn, 2018). In order to evaluate possible differences between these two types of metrics, we included metric type as a moderator in the analysis. However, the correlation of this moderator with others prevented the assessment of its independent effect. While category III measures the recovery after disturbances accounting for its impact on the ecosystems (resistance), category I does not. This does not represent a problem when the complete vegetation cover is destroyed by the disturbance and thus resistance is negligible (e.g. after heavy fires, forest clearing or mining), but does not allow testing for resilience effects that are independent of resistance after low-intensity disturbance. This means that it is possible that for a small number of cases based on category I, the patterns presented here reflect both resistance to and resilience from disturbance. Future analyses should consider this and include only studies in which both resilience and resistance have been quantified.

Finally, not only a proper design but also the ability to continue studies over time is crucial to understanding functional diversity–resilience relationships, especially in ecosystems with slow dynamics and recurrent disturbances (Li et al., 2015). Short-term studies are fundamental to assess the immediate response of ecosystems to disturbances, but they do not always represent the full trajectory of recovery that should be assessed in the long term (de Bello et al., 2020).

5 | CONCLUSIONS

The fundamental mechanisms promoting the resilience of plant communities are a central question in ecology. The present meta-analysis evaluated how the dominance of fast-growing species and the variety of functional traits are related to resilience and, despite the existence of different hypotheses, suggesting a positive relationship between resilience and these different components of functional diversity and the considerable number of studies evaluating resilience quantitatively, no general pattern emerged. In this respect, our findings conform to those of other studies that also failed to detect a consistent relationship between resilience and species richness, both locally and across ecosystems. Overall, this emphasizes existing concerns as to whether species richness is a reliable indicator of ecosystem resilience to environmental change. Moreover, using a trait-based framework instead of species richness to analyse ecosystem resilience also found only limited support. There was some evidence of functional diversity–resilience association, which, however, was strongly context dependent, depending on the type of ecosystem, the response variable analysed (biomass-related variables or floristic composition) and the ecological or methodological characteristics of the studies. Future studies should consider this context dependency, and identify environmental settings under which functional diversity actually confers resilience.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data set and code are available in Zenodo public data repository (DOI: [10.5281/zenodo.10476194](https://doi.org/10.5281/zenodo.10476194)).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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