





The effect of natural disturbances on forest biodiversity: an ecological synthesis

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ABSTRACT

Disturbances alter biodiversity *via* their specific characteristics, including severity and extent in the landscape, which act at different temporal and spatial scales. Biodiversity response to disturbance also depends on the community characteristics and habitat requirements of species. Untangling the mechanistic interplay of these factors has guided disturbance ecology for decades, generating mixed scientific evidence of biodiversity responses to disturbance. Understanding the impact of natural disturbances on biodiversity is increasingly important due to human-induced changes in natural disturbance regimes. In many areas, major natural forest disturbances, such as wildfires, windstorms, and insect outbreaks, are becoming more frequent, intense, severe, and widespread due to climate change and land-use change. Conversely, the suppression of natural disturbances threatens disturbance-dependent biota. Using a meta-analytic approach, we analysed a global data set (with most sampling concentrated in temperate and boreal secondary forests) of species assemblages of 26 taxonomic groups, including plants, animals, and fungi collected from forests affected by wildfires, windstorms, and insect outbreaks. The overall effect of natural disturbances on α -diversity did not differ significantly from zero, but some taxonomic groups responded positively to disturbance, while others tended to respond negatively.

Disturbance was beneficial for taxonomic groups preferring conditions associated with open canopies (e.g. hymenopterans and hoverflies), whereas ground-dwelling groups and/or groups typically associated with shady conditions (e.g. epigeic lichens and mycorrhizal fungi) were more likely to be negatively impacted by disturbance. Across all taxonomic groups, the highest α -diversity in disturbed forest patches occurred under moderate disturbance severity, i.e. with approximately 55% of trees killed by disturbance. We further extended our meta-analysis by applying a unified diversity concept based on Hill numbers to estimate α -diversity changes in different taxonomic groups across a gradient of disturbance severity measured at the stand scale and incorporating other disturbance features. We found that disturbance severity negatively affected diversity for Hill number $q = 0$ but not for $q = 1$ and $q = 2$, indicating that diversity–disturbance relationships are shaped by species relative abundances. Our synthesis of α -diversity was extended by a synthesis of disturbance-induced change in species assemblages, and revealed that disturbance changes the β -diversity of multiple taxonomic groups, including some groups that were not affected at the α -diversity level (birds and woody plants). Finally, we used mixed rarefaction/extrapolation to estimate biodiversity change as a function of the proportion of forests that were disturbed, i.e. the disturbance extent measured at the landscape scale. The comparison of intact and naturally disturbed forests revealed that both types of forests provide habitat for unique species assemblages, whereas species diversity in the mixture of disturbed and undisturbed forests peaked at intermediate values of disturbance extent in the simulated landscape. Hence, the relationship between α -diversity and disturbance severity in disturbed forest stands was strikingly similar to the relationship between species richness and disturbance extent in a landscape consisting of both disturbed and undisturbed forest habitats. This result suggests that both moderate disturbance severity and moderate disturbance extent support the highest levels of biodiversity in contemporary forest landscapes.

Key words: natural disturbance, diversity–disturbance relationship, disturbance severity, disturbance extent, intermediate disturbance hypothesis, forest communities, α -diversity, β -diversity.

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I. INTRODUCTION

Forest ecosystems host considerable terrestrial biodiversity, including many endangered species (Hill *et al.*, 2019). In turn, biodiversity plays a crucial role in forest ecosystem services, such as supporting the production of tree biomass, storing soil carbon, and providing goods and recreational services (Paquette & Messier, 2011; Gamfeldt *et al.*, 2013). Natural disturbances strongly influence biodiversity and can trigger major changes in forest communities (Swanson *et al.*, 2011; Lindenmayer *et al.*, 2019). The frequency, extent, intensity,

and severity of natural disturbances in forest landscapes – such as wildfires, windstorms, and insect outbreaks – is increasing in many parts of the world due to land-use modification and climate change (Seidl *et al.*, 2017; Sommerfeld *et al.*, 2018; Lindenmayer & Taylor, 2020; Collins *et al.*, 2021). Concurrently, the widespread suppression of natural disturbances can be detrimental to disturbance-dependent biota (Cumming, 2005; Hedwall & Mikusiński, 2016). Therefore, detailed knowledge about the response of forest communities to natural disturbances is essential.

Interest in the effects of disturbance and post-disturbance community succession is older than the scientific discipline of ecology itself (King, 1685; Clements, 1916). There are many theories that seek to explain how biodiversity responds to disturbance (e.g. Connell, 1978; Hastings, 1989; Wootton, 1998; reviewed by Pulsford, Lindenmayer & Driscoll, 2016). For instance, the popular but debated intermediate disturbance hypothesis (IDH) posits that diversity peaks at intermediate levels of disturbance frequency or intensity [Grime, 1973; Connell, 1978, but see Fox (2013) for a critique]. In addition to flaws in the theoretical underpinnings of the IDH, empirical studies have shown that relationships between species diversity and natural disturbance are often not hump-shaped but can have various shapes and strengths (Mackey & Currie, 2001; Bongers *et al.*, 2009). It has been hypothesised that disturbance intensity and frequency may have negligible effects on species diversity in communities where succession is driven by ecological processes other than competition (Chesson & Huntly, 1997). The diversity–disturbance relationship may differ depending on the organismal group, with hump-shaped responses for primary producers or sessile organisms, but non-hump-shaped responses for mobile organisms at higher trophic levels (Wootton, 1998). Disturbance effects on diversity are expected to be stronger following severe, infrequent disturbances as opposed to following moderate, more predictable disturbance events, such as regular flooding in riparian ecosystems (Reice, Wissmar & Naiman, 1990). Hence, while there is a plethora of theories and hypotheses, such as the IDH, there is no universal disturbance theory that could apply to different ecosystems, disturbance types, and taxonomic groups.

The characteristics of disturbance such as intensity, severity, and extent are critical in shaping diversity–disturbance relationships (Yeboah & Chen, 2016; Wernberg *et al.*, 2020). However, issues with defining terms as well as difficulties with quantifying disturbance characteristics in natural conditions at multiple spatial scales have impeded untangling the factors that drive the response of biodiversity to disturbance. Disturbance intensity, i.e. the strength of the disturbing force (e.g. the amount of heat produced by the wildfire; Keeley, 2009), can be difficult to quantify; thus this information is often missing in such studies (see Table 1 for definitions of terms). Disturbance severity can be applied more straightforwardly to compare the effects of different disturbance types. Disturbance severity can be quantified as the degree to which pre-disturbance vegetation has been damaged (Pickett & White, 1985). Specifically, to forests as the focus of our study, we considered the severity of a forest disturbance to be the proportion of trees in a stand with a destroyed canopy, which includes individuals of seeder species that are typically killed by disturbance and regenerate from seed as well as resprouter species that mostly survive and can resprout later (Pausas *et al.*, 2004). The term *disturbance severity* describes the impact of disturbance on the forest canopy at the scale of a disturbed forest stand. Conversely, we use the term *disturbance extent* to refer to the proportion of

Table 1. Glossary.

Disturbance intensity	Physical strength of the disturbing force, e.g. the amount of heat produced by a wildfire.
Disturbance severity	The effect of disturbance on an ecosystem, often quantified as the degree to which the pre-disturbance vegetation has been damaged. Herein we define disturbance severity as the proportion of trees with a completely killed canopy, including species typically killed by disturbance that regenerate from seed and resprouter species that mostly survive and can resprout after a disturbance event. The severity as defined here, serves as proxy for the strength of disturbance affecting demographic rates of above- and belowground organisms.
Disturbance extent	The area affected by a disturbance. Herein we quantify disturbance extent as the proportion of disturbed area in a landscape consisting of disturbed and undisturbed forests.
α -diversity	Mean number of species sampled across a set of sampling localities.
β -diversity	The extent of differentiation along habitat gradients according to Whittaker's (1960, 1972) definition. Several concepts and measures of β -diversity exist in the literature. In the present meta-analysis, we use β -diversity when we refer to differences in species composition between disturbed and undisturbed forests.
Mixture diversity	Diversity of a forest where a specified proportion of forest is disturbed, i.e. the diversity in a proportional mixture of disturbed and undisturbed forest.

disturbed habitat at the scale of a landscape where the landscape may have variable proportions of both disturbed and undisturbed forest stands (Fig. 1). Spatial scale of a landscape may vary from few hectares to several square kilometres depending on studied taxa and spatial extent of a particular study.

Disturbance characteristics can have varying effects on different components of biodiversity. Disturbances can increase, decrease or have no impact on the average species richness across a set of sampled localities, i.e. α -diversity (Moretti, Obrist & Duelli, 2004; Ratchford *et al.*, 2005; Nelson, Halpern & Agee, 2008; Wermelinger *et al.*, 2017). However, α -diversity does not reflect the disturbance-induced turnover in species composition, i.e. β -diversity. Extensive disturbances may create homogeneous disturbed areas and thus decrease β -diversity by homogenising species composition (Solar *et al.*, 2015). Conversely, β -diversity may increase if the variation in conditions is high following forest disturbance (Jones & Tingley, 2021). Variation in disturbance severity as well as in time since disturbance could create patchy landscapes with intermediate spatial extent of disturbed areas, resulting in higher biodiversity at the landscape level (Martin & Sapsis, 1992; Moretti *et al.*, 2002).

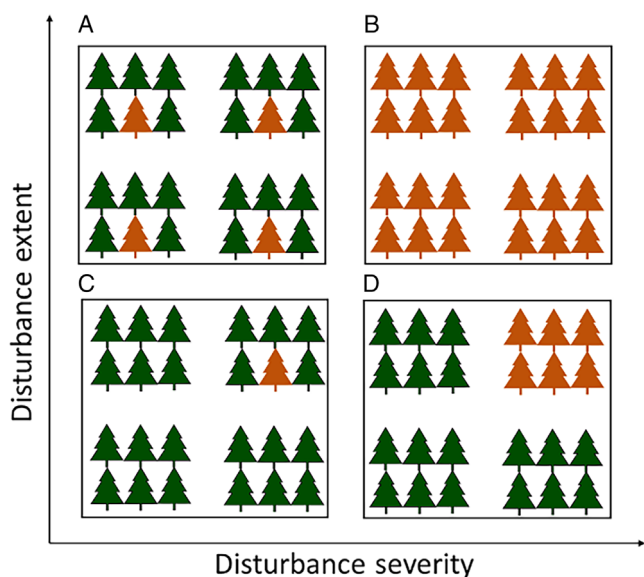


Fig. 1. Schematic representation of four hypothetical landscapes on the gradients of disturbance severity and extent. Each landscape consists of four forest stands. Dark green and brown trees represent undisturbed and disturbed parts of a stand, respectively. (A) Landscape where all stands are disturbed, but the disturbance severity within the stands is low; (B) landscape where all stands are severely disturbed; (C) landscape where most stands have not been affected by disturbance and the disturbance severity within a disturbed stand is low; (D) landscape where most stands have not been affected by disturbance, but the disturbance severity within a disturbed stand is high.

Here, we quantified the effects of natural disturbances on forest biodiversity on a global data set across 26 taxonomic groups, including plants, fungi, and animals from disturbed and undisturbed forests. We investigated the impacts of disturbance severity and extent separately and analysed their effects on different components of biodiversity. First, we predicted that natural disturbance changes α -diversity but that the direction and magnitude of the effect depends on disturbance severity at the stand scale. To assess that expectation, we tested if natural disturbances influence α -diversity of forest-dwelling species by comparing species richness in disturbed and undisturbed forests using a meta-analytic approach. We further tested if and how the response of α -diversity depends on taxonomic group, disturbance severity, disturbance type, and time since disturbance. We predicted that several groups would benefit from disturbance, e.g. saproxylic organisms and groups associated with early successional stages, while groups preferring intact forest may be negatively affected. Additionally, we tested the effects of disturbance characteristics and taxonomic group on the disturbance-induced difference in α -diversity by analysing species diversity calculated from species incidence matrices. Second, we hypothesised that natural disturbance induces changes in community composition and tested if the response of β -diversity, measured as the difference in species

composition between naturally disturbed and undisturbed forests, depends on taxonomic group and disturbance characteristics at the stand scale. Subsequently, we investigated the relationship between species diversity and disturbance extent at the landscape scale by simulating landscapes with variable proportions of disturbed and undisturbed patches. We tested the extent of disturbance at which forest biodiversity peaks, i.e. which level of disturbance extent corresponds to the maximal biodiversity considering both disturbed and undisturbed forest stands. For the latter, we used a mixed rarefaction/extrapolation approach to estimate the biodiversity change as a function of the proportion of disturbed forests on a landscape level (Chao *et al.*, 2019). This procedure allowed us to determine the disturbance extent that maximises diversity in a proportional mixture of disturbed and undisturbed habitats, i.e. maximal mixture diversity. We also tested if and how this level of disturbance extent at the landscape scale varies between taxonomic groups and depends on disturbance characteristics at the stand scale.

II. MATERIALS AND METHODS

(1) Data collection

We followed the guidelines for systematic literature reviews (Pullin & Stewart, 2006) to compile comparisons of species richness in naturally disturbed and undisturbed forests. We restricted our compilation to the three common types of natural forest disturbances: wildfires, windstorms, and insect outbreaks. To be included in our analyses, individual studies had to: (i) examine forests disturbed by wildfires, windstorms, or insect outbreaks; (ii) investigate forests affected by only one of the aforementioned disturbance types; (iii) compare disturbed and undisturbed control plots located in the same forest habitat type – compared disturbed and undisturbed plots had to be similar in size, surveyed with the same methods during the same study period and with the same sampling effort; (iv) provide spatially independent replicates of disturbed and undisturbed forests; (v) contain data about species assemblages (i.e. studies investigating populations of a single species were excluded); and (vi) be field-based case studies (i.e. simulation studies and reviews were excluded).

We screened the *Web of Science* electronic database using the following search string: (forest* OR woodland*) AND (disturb* OR dieback OR wildfire OR fire OR windthrow OR storm OR pest OR ((insect* OR beetle*) AND (outbreak OR attack))) AND ('species richness' OR 'number* of species' OR biodiversity). This resulted in >8000 articles (on 4 August 2020) from which we selected 338 articles after screening the titles and abstracts (see Fig. S1 for the decision workflow). In addition, we added four relevant studies, matching the same criteria, either found in the references of articles or articles that were suggested by authors. These 342 articles were further screened, and 51 studies matched the selection criteria based on the full texts.

To ensure valid effect sizes, we assessed the quality of designs and excluded studies with pseudoreplication, i.e. studies where disturbed and undisturbed plots were not spatially interspersed (Hurlbert, 1984; Halme *et al.*, 2010). The spatial arrangement of plots in all studies was checked based on the description of methods and/or geographic coordinates. We contacted the authors of articles to provide data and to clarify the study designs when necessary.

Mean and standard deviation of the number of species in sampling units as well as the sample sizes in original studies were extracted from published texts, tables, and figures (we used <https://automeris.io/WebPlotDigitizer> for importing values from figures). In addition, we compiled information on covariates including disturbance type, i.e. wildfire, windstorm or insect outbreak, time since disturbance (in years), geographic location of the study area (latitude and longitude), disturbance severity, and taxonomic groups surveyed. Disturbance severity was quantified as the proportion of dead or fatally injured trees, per cent basal area loss or through qualitative indications (see Table S1 for information on all severity levels used in our study). In the few cases where only qualitative estimation was possible, we derived the following severity percentages as described in Appendix A in Leverkus *et al.* (2018b): low severity, 30%; low to moderate, 45%; moderate, 60%; moderate to high or mixed or variable, 75%; high, 90%; and severe, 100%. If the severity varied between study plots, we used the mean severity of plots for each study site, study year or severity category in the analyses (detailed information about methods for quantifying the severity is available in Table S1).

We gathered information describing the conditions of undisturbed control forests (summarised in Table S2). For that purpose, we asked authors to provide the following information: (i) if the control forests were primary or secondary forest; (ii) naturally grown or planted; (iii) the proportion

of non-native tree species; and (iv) the approximate age of the forest stand or a qualitative estimation of the successional phase. Alternatively, if authors could not be contacted, information was found from the source publications and/or the global map of forest classes (Schulze, Malek & Verburg, 2019). Most studies were conducted in secondary forests (68%). However, for 25% of the studies reported as primary forest, small-scale forest management activities such as selective logging and/or agricultural activities such as grazing/browsing within the last 100 years were evident or had possibly occurred. 84% of all control forests were naturally regrown and the proportions of non-native tree species were always reported as <20%, most often <2%; alternatively the proportion was qualitatively described as ‘none to very little’. Control forests in all study sites were typically mature, i.e. reached their typical local size making them ready to be harvested.

We compiled a database of species abundances/presences consisting of raw data underpinning the published studies. Authors of the respective studies provided raw data if not already available as supplementary material or in data repositories. Our final database consisted of 317 community matrices and included the following species groups: amphibians, ants, bats, birds, epigeic lichens, epigeic bryophytes, epigeic arachnids (spiders and harvestmen), hemipterans, herbaceous vascular plants, hoverflies (Syrphidae) and bee flies (Bombyliidae), hymenopterans (excluding ants), lacewings, lepidopterans (butterflies and moths), molluscs, mycorrhizal fungi, non-saproxyllic beetles, parasitoids (all recruited from Hymenoptera), reptiles, saproxyllic beetles, saproxyllic fungi, shrews, soil fauna (including soil-inhabiting springtails, oribatid mites and earthworms), tree-associated (epiphytic and epixylic) bryophytes, tree-associated (epixylic) lichens, and woody plants (trees and shrubs). Note that not all data from the meta-analysis of mean species richness were

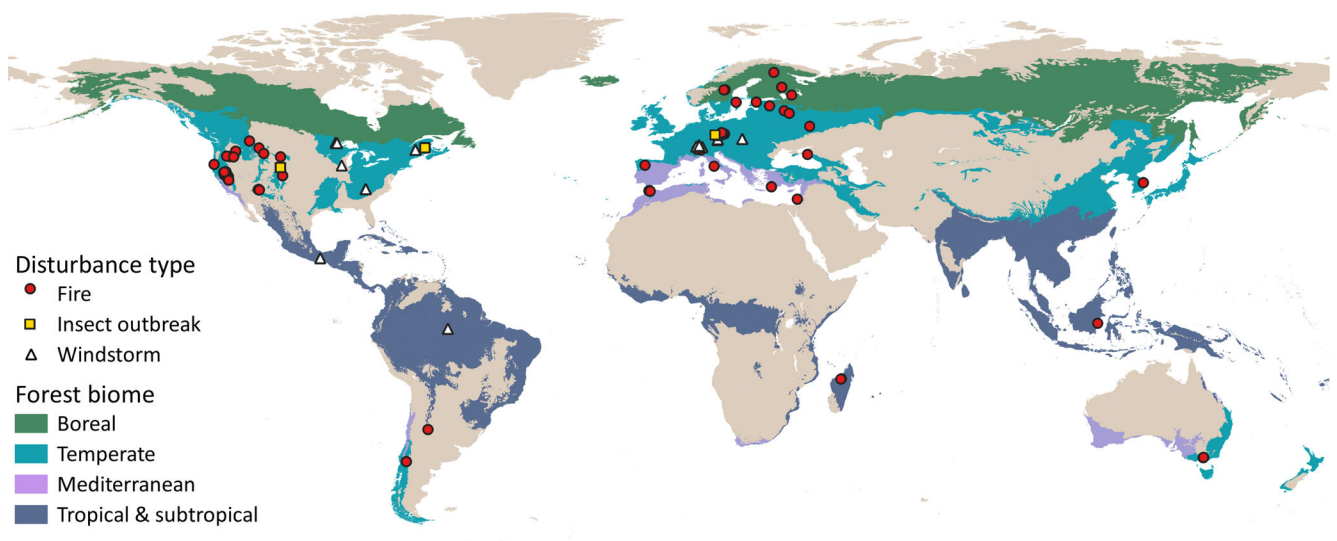


Fig. 2. The locations of study sites ($N = 70$) included in the meta-analysis. Classification of biomes is based on Olson *et al.* (2001).

underpinned by original raw data sets. One taxonomic group, stoneflies, was not supported by raw data and thus were included only in the meta-analysis of mean species richness. To account for differences among forests belonging to different biomes, each study site was classified as boreal, temperate, mediterranean, or subtropical/tropical using the classification of biomes in Olson *et al.* (2001) and the authors' specifications (see Fig. 2).

(2) Analysis of α -diversity

We applied two approaches to analyse the effects of natural disturbances on α -diversity: a meta-analysis of mean species richness and an analysis of species diversity quantified using Hill numbers. Hill numbers are a mathematically unified family of diversity measures that incorporate relative abundance and species richness. They are expressed in units of effective numbers of species, i.e. the number of equally abundant species that would be necessary to give the same value of a diversity measure (Chao *et al.*, 2014). For comparing mean numbers of species between naturally disturbed and undisturbed plots, we used the log response ratio (lnR) of species richness between the naturally disturbed plots (treatment group) and undisturbed plots (control group). The lnR describes the proportional difference in species richness between control and treatment groups. The natural logarithm transformation of the response ratio both linearises the metric, treating deviations in the denominator and the numerator as equal, and normalises its otherwise skewed distribution (Hedges, Gurevitch & Curtis, 1999). The meta-estimate of lnR across a set of studies can be back-transformed to per cent differences between treatment and control groups, providing an intuitively accessible effect size value.

We fitted two types of models. First, we conducted a random-effects meta-analysis to assess if the overall effect of natural disturbance on species richness differed from zero. For that purpose, we fitted only the intercept (i.e. the overall mean effect size measured as lnR) and random effects. To quantify heterogeneity in this model, we used the Q statistic (Viechtbauer, 2010). The identity of a case study and its geographic coordinates were included as random effects in the model to control for unmeasured specificities of sampling design and study area as well as for spatial and temporal autocorrelation. This means that multiple data points per study were included if studies examined multiple taxonomic groups, if surveys lasted for more than 1 year, or if they investigated multiple disturbance types (affecting different study plots) or different ranges of disturbance severities. To account for dependent effect sizes caused by the same control group being shared between different disturbed plots (differing either in disturbance severity or in time since disturbance), we calculated the corrected variance–covariance matrix and used this as a component of sampling variance meta-regression models (Lajeunesse, 2011).

Second, we examined if and how the effect of disturbance depends on taxonomic group, characteristics of disturbance, and the study system. For that purpose, we conducted a mixed-effects meta-analysis by adding the fixed moderators (i.e. effect modifiers) to the model described above. These fixed moderators included the taxonomic group, disturbance type, and forest biome as categorical variables. Disturbance severity and time since disturbance (years) were included as quantitative variables. Time since disturbance was log-transformed to improve normality. Both numeric variables were centred by subtracting the mean. We also included the quadratic terms of time since disturbance and disturbance severity to test the non-linear relationship with the lnR. We subtracted the intercept from the effect sizes (by including -1 in the model formula). We obtained the significance of effect modifiers from Q tests covering all the parameters related to a given factor (Viechtbauer, 2010). In the final model, we used an omnibus test of moderators (Q_M) to assess the null hypothesis that all coefficients except the intercept were simultaneously zero, and a further test (Q_E) to assess the significance of residual heterogeneity. We considered all effects significant at $P \leq 0.05$.

We estimated species diversity for Hill numbers $q = 0, 1, \text{ and } 2$ based on 95% sample coverage for disturbed and undisturbed plots, based on species incidence (Chao *et al.*, 2014). This procedure allowed us to compare observed levels of α -diversity to levels of α -diversity standardised by sampling effort. Furthermore, the statistical framework based on Hill numbers reveals the importance of species relative abundance in responding to disturbance, i.e. whether disturbance effects on α -diversity were predominantly driven by rare, common or dominant species [Chao *et al.*, 2020; see Thorn *et al.*, 2020a and Georgiev *et al.*, 2020 for a similar application of the Hill framework]. We calculated the difference between estimated Hill numbers as lnR between naturally disturbed and undisturbed plots. We further used this as a response variable in the linear mixed-effects model including taxonomic group, disturbance type, and forest biome as categorical variables. Disturbance severity and time since disturbance (years) were included as quantitative variables. Time since disturbance was log-transformed to improve normality. Both numeric variables were centred by subtracting the mean. We also included the quadratic terms of time since disturbance and disturbance severity to test the non-linear relationship with the lnR. We subtracted the intercept from the effect sizes (by including -1 in the model formula). The identity of a case study and study site were included as random effects.

All analyses were conducted in R 4.0.4 (R Core Team, 2021). We used the *rma.mv* function in the *metafor* package (Viechtbauer, 2010) for building and testing the multi-level linear mixed models. lnR values were weighted by the corresponding sampling variance within the statistical model. Hill numbers for specified sample coverage were calculated using the *estimateD* function in the *iNEXT* package (Hsieh, Ma & Chao, 2016).

(3) Analysis of β -diversity

We used original raw data matrices to examine changes in community composition induced by natural disturbance. A raw data matrix consisted of presences and absences of species in all study plots sampled in one case study in the same study site and during the same year since disturbance, for both disturbed and undisturbed forests. For testing differences in community composition between disturbed and undisturbed forests, we conducted permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017). The PERMANOVA was based on matrices of Jaccard distances and performed using the function *adonis2* in the *vegan* package (Oksanen *et al.*, 2019). This analysis provides a pseudo *F*-value, based on 999 permutations, that quantifies the deviance from the null hypothesis (which states that composition is the same between disturbed and undisturbed forest), while simultaneously accounting for imbalanced study designs (McArdle & Anderson, 2001). Consequently, larger pseudo *F*-values correspond to larger changes in community composition resulting from natural disturbance. This pseudo *F*-value represents the standardised difference between communities in disturbed and undisturbed plots within a single presence–absence matrix. We restricted this analysis to those matrices that yielded pseudo *F*-values over the course of permutations. For this purpose, those matrices that generated fewer than 99 permutations were excluded. These restrictions resulted in a total of 209 matrices, which provided pseudo *F*-values for the analysis described below.

To test if natural disturbance affected community composition, we modelled pseudo *F*-values using linear mixed models with the *lmer* function in the *lme4* package (Bates *et al.*, 2015). To test if the association depended on the characteristics of the disturbance and the study system, we included the taxonomic group, disturbance type and forest biome as categorical predictors, and disturbance severity and time since disturbance as numerical covariates. For the analysis of β -diversity, we included the study identity and study site as random effects to control for possible differences among study sites and repeated measurements within one study site. We omitted the intercept from the model formula to determine if pseudo *F*-values differed significantly from zero. Therefore, significant changes in community composition due to natural disturbance were indicated by pseudo *F*-values significantly larger than zero.

(4) Analysis of mixture diversity

We estimated species diversity associated with landscapes within which a given proportion of forest was affected by disturbance using a mixed rarefaction/extrapolation approach based on Hill numbers (Hill, 1973; Chao *et al.*, 2019; for an application see Thorn *et al.*, 2020b). The method extends classical rarefaction and extrapolation towards a proportional mixture of two rarefaction/extrapolation curves derived from two distinct species

assemblages (Chao *et al.*, 2014, 2019). The mixed rarefaction/extrapolation was based on plots surveyed in undisturbed forests (t1) and plots surveyed in corresponding disturbed forests (t2). When a proportion of undisturbed plots (e.g. t1a) are disturbed by a natural disturbance, it is equivalent to replacing these t1a plots with the same number of plots randomly selected from disturbed forests. Using a mixture of rarefaction and extrapolation, we analytically retrieved the species richness of mixed assemblages and assessed species compositions (i.e. the number of unique and shared species). In addition to this, mixed rarefaction/extrapolation allowed estimating the proportions of disturbed and undisturbed plots corresponding to certain values of species richness. These values of species richness include the numbers of species unique to disturbed or undisturbed forests as well as the numbers of species that are shared between disturbed and undisturbed forests. By summing the richness of unique species and shared species, the total landscape-level species richness of the proportional mixture can be calculated for each proportional mixture of disturbed and undisturbed forests.

The proportion of plots affected by disturbance can subsequently be used as a proxy for the proportion of forest area affected by disturbance (Chao *et al.*, 2019; Thorn *et al.*, 2020b). Mixed rarefaction/extrapolation is based on comparisons of plots randomly selected from any location of a study design and is independent of plot size and the number of plots within a respective study, as long as all plots within a study are of similar sizes. The independence from the sizes of the areas is particularly important as detailed information about the size of a disturbed area for each study year was not available. We plotted the mixture diversity as well as the numbers of species unique to disturbed and undisturbed forests against the proportion of disturbed forest and fitted curves using LOESS (local polynomial regression) by means of the basic *loess* function in R with the *family* argument set as ‘symmetric’ to obtain more robust curves, i.e. to reduce the impact of possible outliers. We further estimated the proportion of disturbed forest area that is associated with the maximal levels of mixture diversity for each individual species matrix (i.e. per each taxonomic group in a study site and particular year after disturbance). The analyses were conducted using the R code miNEXT (mixed iNterpolation/EXTrapolation, available at <https://github.com/AnneChao>).

We tested the effect of disturbance type, taxonomic group, forest biome, disturbance severity, and time since disturbance on the proportion of disturbed forest associated with the highest mixture diversity per data set. For that purpose, we used beta regression by means of the function *gam* with the *family* argument set to *betar* and logit-link function in the R-package *mgcv* (Wood, Pya & Saeften, 2016). We subtracted the intercept from the effect sizes (by including -1 in the model formula) to evaluate if effects differed significantly from 50% of plots affected by disturbance. To make the coefficients of the model interpretable, we included

non-numerical covariates as random factors and centred the numerical covariates: disturbance severity and time since disturbance. We also controlled for study identity and study site by including these variables as random effects.

III. RESULTS

Our analysis of α -diversity was based on 508 data points, with comparisons between disturbed and undisturbed forests in 70 different study sites derived from 51 studies (Fig. 2). Most studies were conducted in boreal and temperate biomes

(82%), with relatively few (18%) in mediterranean and tropical regions (Figs 2 and S2). Wildfires were the most commonly investigated disturbance (33 studies, 381 data points), followed by windstorms (15 studies, 98 data points) and insect outbreaks (4 studies, 29 data points). Among the 26 taxonomic groups, herbaceous and woody vascular plants were the most widely studied groups (13 studies, 98 data points and 11 studies, 97 data points, respectively), followed by non-saproxyltic beetles (9 studies, 28 data points). Early years after disturbance were studied most often – of the 508 data points, 377 covered 10 years or less, 94 represented 11–20 years and 37 data points addressed more than 20 years after disturbance. The numbers of individual studies

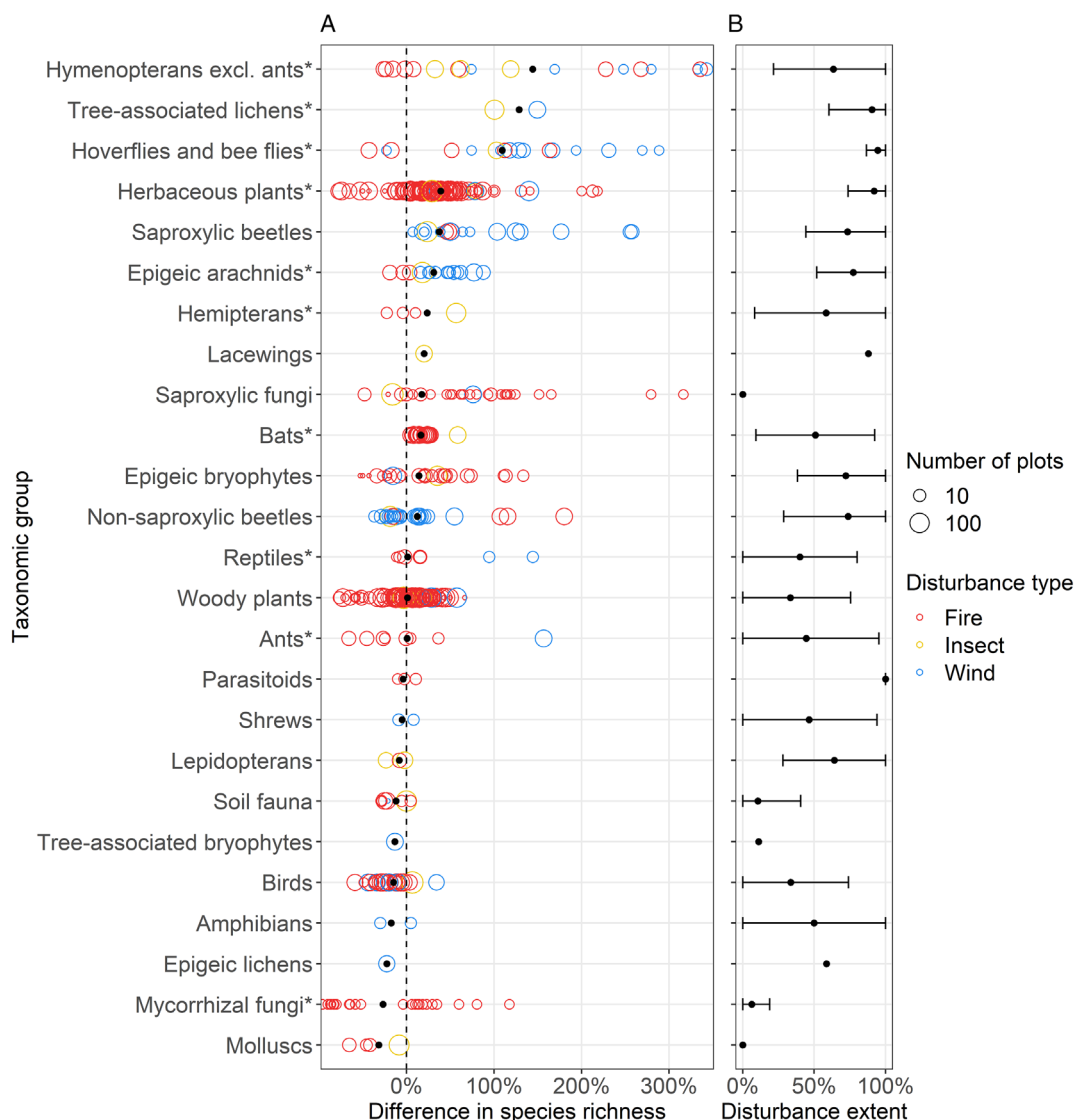


Fig. 3. Differences in α -diversity between naturally disturbed and undisturbed forests categorised by taxonomic group. (A) Black dots represent weighted mean effect sizes transformed to percentage differences in species richness, coloured circles correspond to each data point. Asterisks against group names indicate significant effects ($p < 0.05$) in the mixed-effects meta-analysis. (B) Proportions of disturbed forest that correspond to the maximal mixture diversity of each taxonomic group. Dots represent the means of data points and whiskers show respective standard deviations. Whiskers are missing when only one incidence matrix for a taxonomic group was available.

per range of years were 46, 16, and 10, respectively. In the analyses of β -diversity and mixture diversity, we used 209 and 297 full species-by-plot abundance matrices, respectively. These subsets were similar in the aforementioned aspects – covering primarily boreal and temperate biomes, wildfires, and vascular plants collected within 20 years since disturbance.

(1) Effect of natural disturbance on α -diversity

Across all taxa, disturbance types, disturbance severities, forest biomes, and time after disturbance, the effect of natural disturbance on α -diversity did not differ significantly from zero ($z = -0.127$; $p = 0.899$). There was high heterogeneity

Table 2. Results of mixed-effects meta-analysis of the effect of natural disturbances on α -diversity. The response variable is the difference in mean species numbers between disturbed and undisturbed forests, quantified as $\ln R$. Q_M = omnibus test for all the parameters in the model; Q_E = test for residual heterogeneity.

Tested moderator	Q	df	p
Disturbance severity	195.30	1	<0.001
Disturbance severity ²	98.31	1	<0.001
Time since disturbance	1.29	1	0.256
Time since disturbance ²	41.51	1	<0.001
Taxonomic group	862.71	26	<0.001
Disturbance type	2.54	2	0.28
Forest biome	12.05	3	0.007
Full model			
Q_M	1099.54	35	<0.001
Q_E	3953.33	461	<0.001

Bold values indicate significant effects ($p < 0.05$).

among studies in this model ($Q = 5915.39$; degrees of freedom [df] = 495; $p < 0.001$), meaning that the effect of disturbance varied considerably among studies.

The mixed-effects meta-analysis showed that the impacts of natural disturbance on α -diversity varied among taxonomic groups (Fig. 3; Table S3) and depended on disturbance severity and time since disturbance (Table 2). The relationships between α -diversity and the quadratic terms of disturbance severity and time since disturbance were negative, indicating hump-shaped relationships with the standardised difference in mean species richness. The positive effect of disturbance on α -diversity peaked at $\sim 55\%$ disturbance severity and decreased thereafter (Fig. 4A). Time since disturbance moderated the effect of disturbance on α -diversity by driving it towards a positive direction from about 2–3 years after the disturbance event and reaching a maximum around 10 years post-disturbance (Fig. 4B). Forest biome moderated disturbance effects: the impact was more

Table 3. Type III analysis of variance table of the results of the linear mixed-effects model with pseudo F -value as response variable. Pseudo F represents a disturbance-induced difference in species composition. Note that F -values in the table are F -statistics from the Type III analysis of variance (not pseudo F -values).

Explanatory variable	F	df	p
Taxonomic group	2.97	23	<0.001
Disturbance type	0.84	2	0.445
Forest biome	0.58	3	0.634
Disturbance severity	2.51	1	0.116
Time since disturbance	1.11	1	0.295

Bold values indicate significant effects ($p < 0.05$).

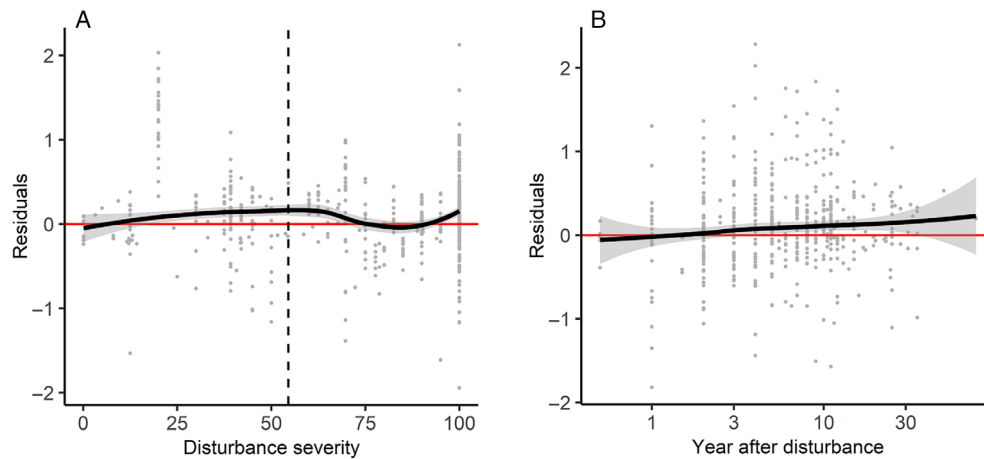


Fig. 4. The residuals of the models explaining the effect of natural disturbance on α -diversity using mixed-effects meta-analysis plotted against (A) disturbance severity, and (B) time since disturbance (year is logarithmic and then back-transformed for easier readability). Descriptions of full models are provided in Section II.(2). Residuals in A result from the full model excluding disturbance severity. Residuals in B result from the full model excluding the time since disturbance. The curves and confidence intervals (shading) are generated by fitting the LOESS function. The dashed vertical line marks the maximal value of α -diversity in disturbed plots that remained unexplained by other moderators except disturbance severity, i.e. the predicted value of disturbance severity that corresponds to the maximal α -diversity.

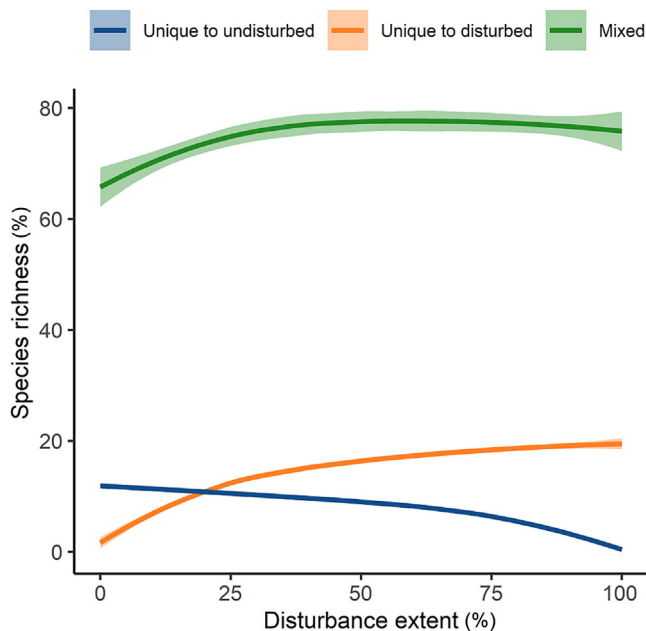


Fig. 5. Response of species richness to the proportion of disturbed area in the forest landscape. The curves and confidence intervals (shading) are generated by fitting the LOESS function. Components of species richness: species unique to disturbed forests; species unique to undisturbed forests; a mixture of both groups of unique species and species shared between two habitat types, i.e. mixture diversity.

Table 4. Results of the beta-regression with the proportion of disturbed forest corresponding to highest mixture diversity as a response variable. Wald tests on terms were applied to test for significance.

Explanatory variable	χ^2	df	<i>p</i>
Taxonomic group	49.908	25	0.002
Disturbance type	2.743	2	0.077
Forest biome	4.459	3	0.037
Disturbance severity	1.372	1	0.242
Time since disturbance	5.285	1	0.022

Bold values indicate significant effects ($p < 0.05$).

negative in mediterranean forests compared to temperate and boreal forests (Tables 2 and S3; Fig. S2). Disturbance type did not significantly moderate the effect of disturbance (Table 2).

Our analysis of disturbance effects on biodiversity quantified using Hill numbers ($q = 0, 1, 2$) for 95% of sample coverage showed that the findings described above were largely driven by species relative abundance. We found that $\ln R$ for $q = 0$ was negatively associated with disturbance severity ($z = -2.55$; $p = 0.01$; Table S4). $\ln R$ of all three Hill numbers depended significantly on the forest biome (Tables S4–S9; Figs S3–S5). There were significant positive effects of disturbance on $\ln R$ for the following taxonomic groups: hymenopterans (excluding ants), hoverflies and bee flies, herbaceous plants, non-saproxyllic beetles (for $q = 0$ only), and saproxyllic beetles.

(2) Effect of natural disturbance on β -diversity

Natural disturbance was associated with significant changes in the species compositions of six taxonomic groups (Table S10): epigeic arachnids ($z = 2.07$; $p = 0.038$), birds ($z = 3.66$; $p < 0.001$), tree-associated (epixylic) lichens ($z = 2.93$; $p = 0.003$), woody plants ($z = 2.86$; $p = 0.004$), herbaceous plants ($z = 2.25$; $p = 0.024$), and ants ($z = 2.11$; $p = 0.035$). Disturbance type, forest biome, disturbance severity, and time since disturbance did not significantly modulate the effects of disturbance on species composition (Table 3).

(3) Relationship between disturbance extent and mixture diversity

Mixture diversity (encompassing species unique to disturbed and undisturbed forest as well as shared species) peaked at ~60% of disturbed forest (Fig. 5) but varied considerably among taxa (Fig. 3B). Beta-regression showed that disturbance extent (i.e. the proportion of forest that was disturbed) corresponding to the highest mixture diversity differed significantly among taxonomic groups (Tables 4 and S11). The disturbance extent corresponding to the highest mixture diversity was significantly larger than 50% for hymenopterans (excl. ants) (at 77% of disturbed forest; $p < 0.001$), hoverflies and bee flies (at 76% of disturbed forest; $p = 0.004$) and reptiles (at 76% of disturbed forest; $p = 0.034$). The disturbance extent corresponding to the highest mixture diversity was greater for longer times since disturbance (Tables 4 and S11).

IV. DISCUSSION

(1) Overall effect and differences among taxonomic groups

Our global meta-analysis (with most sampling concentrated in boreal and temperate biomes), showed that the overall effect of natural disturbance on forest α -diversity did not differ significantly from zero. However, the responses varied significantly among taxonomic groups, and while many groups benefited from disturbance, several others were negatively impacted, possibly due to different disturbance response strategies (Moretti & Legg, 2009; Pausas, 2019). For example, flower-visiting hymenopterans and flies were among the taxa that benefited from natural disturbance, possibly because of the increased availability of nectar and pollen resources and warmer microclimatic conditions caused by enhanced canopy openness at early successional stages (Proctor *et al.*, 2012; Rodríguez & Kouki, 2017; Ramos-Fabiell *et al.*, 2018). Our finding is consistent with a meta-analysis on the effect of fire on pollinators that revealed positive responses of this group to wildfire (Carbone *et al.*, 2019). Conversely, ground-dwelling taxa and/or groups typically associated with shady conditions, such as epigeic lichens,

and mycorrhizal fungi, tended to be more often negatively affected by disturbances (Moretti *et al.*, 2004). Mycorrhizal fungi possibly also additionally suffered from the death of host trees poorly adapted to severe wildfires (Franco-Manchón *et al.*, 2019).

Previous studies have often reported positive multi-taxa responses to natural disturbances. In a previous meta-analysis investigating disturbance effects on temperate and boreal forest ecosystems, Thom & Seidl (2015) found that stand-replacing natural disturbances increased species richness by 36% on average. They concluded that the impact of disturbance was variable, with some studies in their data set reporting negative effects of disturbances on some elements of biodiversity, but the overall response of biodiversity to disturbance was positive (Thom & Seidl, 2015). The high variability in multi-taxa responses, including taxa identified by sequencing, resulting in the absence of an overall effect of disturbance, has been previously found in forests affected by bark beetles (Kortmann *et al.*, 2021). Another study on multi-taxa responses to bark beetle disturbance reported a positive overall effect on biodiversity (Beudert *et al.*, 2015). However, differences in the response to disturbance have not been tested previously for such a wide variety of taxonomic groups and ecosystems as in our meta-analysis. Our study shows that the heterogeneity of responses to disturbances in a large global data set prevails over possible directional effects in smaller subsets of taxa.

In the analysis of α -diversity using Hill numbers and accounting for sample coverage, differences between diversities in disturbed and undisturbed forests for most taxonomic groups were non-significant. Natural disturbances significantly increased the diversity of hymenopterans, hoverflies (Syrphidae) and bee flies (Bombyliidae), saproxylic beetles, non-saproxylic beetles, and herbaceous plant species (for $q = 0$). The list of positively affected taxonomic groups was almost identical for $q = 1$ and $q = 2$, excluding only non-saproxylic beetles. The higher diversity of saproxylic beetles in disturbed compared to undisturbed plots is not surprising, as saproxylic beetles benefit from abundant dead wood and warm microclimates (Seibold *et al.*, 2016, 2021). It is possible that the higher diversity of herbaceous plants in disturbed plots due to open canopy conditions at least partly explains the high numbers of flower-visiting Hymenoptera and Diptera, as well as non-saproxylic beetle species. Bees, the most widely studied group within Hymenoptera, benefit from diverse plant communities, which provide a variety of nectar resources and support bees during longer vegetative periods (Rubene, Schroeder & Ranius, 2015; Rhoades *et al.*, 2018). A considerable number of non-saproxylic beetles are herbivores that may also benefit from higher plant diversity. The other large group of non-saproxylic beetles was composed of mainly carnivorous ground beetles (Carabidae) that may benefit from the abundance of other invertebrates as well as the variety of microhabitats created by natural disturbances (Barber & Widick, 2017). The lack of statistically significant disturbance effects for several other taxa in this additional analysis indicates the substantial role of species relative

abundances in shaping diversity–disturbance relationships of different taxonomic groups.

The effect of a natural disturbance on biodiversity may depend on the pre-disturbance condition of the forest (Donato, Campbell & Franklin, 2012; Lindenmayer *et al.*, 2019). In our synthesis, an undisturbed control forest provided a proxy for the pre-disturbance state of a respective disturbed forest. Forest management intensity is one of the important aspects that could potentially moderate the contrast in species richness between naturally disturbed and control forests. However, the vast majority of forests in our data set were relatively homogenous in management intensity and stand age, with most having experienced weak to moderate management activities and were in intermediate to late successional stages (summarised in Table S2). This prevented us from investigating the effect of pre-disturbance conditions on the outcomes of forest disturbance on biodiversity.

(2) The effects of disturbance severity and extent

Our results suggest that moderate disturbance severity and moderate disturbance extent were associated with maximum overall levels of biodiversity at the stand and landscape scale, respectively. Our meta-analysis showed that the highest levels of α -diversity in disturbed stands were associated with forests in which slightly more than half of the trees (~55%) had canopies destroyed by disturbance; α -diversity declined when the severity increased further (see Table 1 for the definition of disturbance severity). The hump-shaped relationship found in our study is in accordance with the relationship predicted by the intermediate disturbance hypothesis (Connell, 1978). The hump-shaped relationship can be explained by potentially higher structural complexity in moderately disturbed stands contributing to higher diversity of microhabitat conditions and resources compared to more homogeneously disturbed or nearly undisturbed stands (Stein, Gerstner & Kreft, 2014; Senf *et al.*, 2020). That is, disturbances with intermediate severity may be associated with higher 'disturbance diversity' that can be related to higher biodiversity as proposed by the pyrodiversity–biodiversity hypothesis (Martin & Sapsis, 1992; Jones & Tingley, 2021; Steel *et al.*, 2021). Some case studies showing that intermediate fire severity can lead to higher pyrodiversity and consequently enhance biodiversity provide support for that explanation (Ponisio *et al.*, 2016; Lazarina *et al.*, 2019). However, the relationship between α -diversity and disturbance severity was not hump-shaped when standardising for sampling effort. The effect was linear negative for $q = 0$, indicating that rare species are more likely to be negatively affected by severe disturbances and/or severely disturbed forests are dominated by few abundant disturbance-favoured species. This finding is in line with the results of case studies, demonstrating that rare species were most affected by post-disturbance management, regardless of taxonomic group (Thorn *et al.*, 2020a). This could be explained by the higher probability that rare species become extinct from a local site, while common and dominant species often have a higher probability of colonising a given site (Chao

et al., 2019). While rare species are more likely to be affected by stochastic processes such as chance of colonisation, random extinction and ecological drift, common and dominant species are more likely to be affected by deterministic processes including environmental filtering, and biotic interactions (Chase & Myers, 2011).

The availability of habitat patches in different successional stages may also result in high biodiversity levels at the landscape scale (Fahrig, 2020). This explanation is also supported by our mixed rarefaction/extrapolation approach, which showed that the overall maximal mixture diversity corresponded to disturbance extents that were close to intermediate, indicating that disturbed and undisturbed patches were both present at similar amounts. Our mixed rarefaction/extrapolation approach showed that the mixture diversity peaked at 60% disturbed forest within the landscape. Similar to the relationship between α -diversity and disturbance severity, the maximal mixture diversity corresponded to a disturbance extent that was moderate, but somewhat higher than intermediate. The latter might be explained by the contribution of species-rich taxonomic groups that peaked at the maximal extent of disturbance, such as herbaceous plants. However, some disturbance-intolerant taxonomic groups, such as soil fauna and molluscs, were associated with low disturbance extent. Hence, attention should be paid not only to the peak in total diversity, but also to certain taxonomic groups and species of conservation concern.

Several recent studies have suggested that disturbance regimes of moderate extent and severity were predominant in temperate and boreal forests in the past (Stueve *et al.*, 2011; Nagel *et al.*, 2017; Čada *et al.*, 2020). Assuming that local species are adapted to historical disturbance regimes, such regimes could be expected to support the highest levels of biodiversity. However, disturbance severity can be highly variable even in the case of catastrophic disturbances, so that considerable amounts of the area can persist relatively unchanged. For example, extensive fires in Yellowstone National Park in 1988, covering thousands of square kilometres, resulted in heterogeneous burn-severity mosaics across which most of the burned area was <200 m from unburned forest edges (Turner *et al.*, 1994). Analyses of the 2019/2020 megafires in south-eastern Australia also showed that despite being greater in extent, these were not proportionally more severe than previous fires in the same area (Collins *et al.*, 2021). Nevertheless, the maximum size of high-severity patches was positively correlated with the extent of burned area. Moreover, the areas affected by megafires are becoming more homogenous, due to decreasing heterogeneity of unburnt patches as shown by recent analysis (Mackey *et al.*, 2021). Therefore, current large and extreme fires can have substantial impacts on ecosystems due to their proportionally higher burn severity and homogenising effect on forest landscapes.

Most study sites included in our synthesis were in temperate and boreal forests and investigated the effects of wildfires or windstorms; studies from other biomes and other disturbance types, matching our selection criteria, were noticeably less common. Therefore, the effects of disturbance on

biodiversity reported here mainly reflect these regions and disturbance types. The biases in the geographical distribution of disturbance types are partly natural, because certain disturbance types are more common in specific ecosystems. For example, wildfires, while being common disturbances in boreal forests, rarely occur naturally in tropical rainforests. Increasingly severe droughts induced by the El Niño Southern Oscillation (ENSO), however, have been associated with more frequent large-scale forest fire events in tropical rainforests in Asia and South America (Alencar, Solorzano & Nepstad, 2004; Gu *et al.*, 2020). Future studies investigating various types of disturbances, especially in tropical areas, would provide a valuable addition to our current knowledge.

(3) The role of time since disturbance

In addition to revealing the effect of disturbance severity, our meta-analysis identified a temporal change in the effect of disturbance on α -diversity. Consistent with previous studies investigating post-disturbance successional change, our results suggested a hump-shaped relationship between time and biodiversity (Yeboah & Chen, 2016; Hilmers *et al.*, 2018). According to our results, species richness in disturbed habitats tends to be similar to undisturbed habitat during the first years after disturbance. Thereafter, the species richness of disturbed habitats starts to increase, possibly because of colonisation through dispersal from surrounding habitats, as well as population expansion of species that survived the disturbance but remained undetected in early post-disturbance surveys because of their rarity or small size (Banks *et al.*, 2017). We found that the overall species richness in a disturbed forest reaches a plateau around 10 years after disturbance. The subsequent addition of competitive species may exclude early successional species so that species richness does not increase at the following stages while it may increase again in old-growth forests (Hilmers *et al.*, 2018).

Our results also showed that the disturbance extent corresponding to maximal diversity can increase with time since disturbance. More extensive areas of disturbed forest possibly provide suitable conditions for disturbance-dependent communities for longer periods. However, early post-disturbance conditions can be temporary and the long-term persistence of such habitats in the landscape may require further disturbances. The disturbance extent that would maintain maximal biodiversity at a greater timeframe than that covered by our study may be significantly lower than 60%. This is because the continuous presence of early successional disturbed forest covering more than half of an entire forest landscape would be the outcome of very high rates of disturbance and would probably result in drastic structural homogenisation (e.g. the loss of large old trees) and the loss of late-successional forest (Senf *et al.*, 2020). The availability of late-successional stages in a landscape is crucial for a variety of specialist taxa of late-successional forests maintaining diversity through the admixture of late-successional species (Bell, Lechowicz & Waterway, 2000; Komonen, 2001; Zhang, Kissling & He, 2013; Solar *et al.*, 2015; Watson *et al.*, 2018). Moreover, the structure and composition of

early successional forests is affected by pre-disturbance age and condition (Franklin *et al.*, 2000; Donato *et al.*, 2012; Lindenmayer *et al.*, 2019), and increasingly by anthropogenic post-disturbance management such as salvage logging (Leverkus *et al.*, 2018a). Therefore, for the persistence of high biodiversity, it is important that natural disturbances contribute to the successional heterogeneity of forest landscapes.

V. CONCLUSIONS

- (1) We found an overall neutral effect of natural disturbance on forest α -diversity, most probably due to highly variable responses of different taxonomic groups. Groups benefiting from disturbances include organisms that prefer conditions associated with open canopies. Conversely, groups associated with a ground-dwelling lifestyle and/or preference for shady conditions tended to be negatively impacted by disturbance.
- (2) The degree of disturbance severity maximising α -diversity at the stand scale was similar to the degree of disturbance extent maximising the diversity in a proportional mixture of disturbed and undisturbed forests at the landscape scale, with both results suggesting that moderate disturbances support the highest levels of overall biodiversity.
- (3) Species richness reached its highest values around 10 years after the disturbance, highlighting the importance of time since disturbance in moderating the effect of disturbance on α -diversity.
- (4) Natural disturbance significantly affected the species composition of six taxonomic groups (ants, birds, epigeic arachnids, epixylic lichens, and herbaceous and woody plants). By contrast, disturbance type and severity, forest biome, and time since disturbance did not modulate β -diversity.
- (5) Future studies on the effects of natural disturbances on biodiversity, especially focusing on rare species, less frequently studied disturbance types, and the tropical biome, could provide valuable novel information.

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VII. DATA AVAILABILITY STATEMENT

Original raw data will be made available by data owners on reasonable request.

VIII. REFERENCES

- References identified with an asterisk (*) provided data used in the meta-analysis; a dagger symbol (†) indicates additional references used only in the supporting information.
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IX. SUPPORTING INFORMATION

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

Fig. S1. PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analyses) diagram representing the flow of information through the decision process (i.e. the number of studies identified, rejected, and accepted).

Table S1. The levels of disturbance severity used in the meta-analysis for quantifying disturbance severity at each study site.

Table S2. Characteristics of undisturbed control forests in all study sites included in the meta-analysis.

Fig. S2. Differences in α -diversity between naturally disturbed and undisturbed forests categorised by taxonomic group.

Table S3. Results of the mixed-effects meta-analysis.

Table S4. Results of the generalised linear mixed models analysing the natural disturbance effects on species diversity (Hill number, $q = 0$) with 95% sampling coverage.

Table S5. Results of the generalised linear mixed models analysing the natural disturbance effects on species diversity (Hill number, $q = 0$) with 95% sampling coverage (same model as in Table S4).

Fig. S3. Differences in diversity of all species ($q = 0$) between naturally disturbed and undisturbed forests categorised by taxonomic group.

Table S6. Results of the generalised linear mixed models analysing the natural disturbance effects on species diversity (Hill number, $q = 1$) with 95% sampling coverage.

Table S7. Results of the generalised linear mixed models analysing the natural disturbance effects on species diversity

(Hill number, $q = 1$) with 95% sampling coverage (same model as in Table S6).

Fig. S4. Differences in diversity of common species ($q = 1$) between naturally disturbed and undisturbed forests categorised by taxonomic group.

Table S8. Results of the generalised linear mixed models analysing the natural disturbance effects on species diversity (Hill number, $q = 2$) with 95% sampling coverage.

Table S9. Results of the generalised linear mixed models analysing the natural disturbance effects on species diversity (Hill number, $q = 2$) with 95% sampling coverage (same model as in Table S8).

Fig. S5. Differences in diversity of dominant species ($q = 2$) between naturally disturbed and undisturbed forests categorised by taxonomic group.

Table S10. Results of linear mixed-effects model with pseudo F -value as the response variable.

Table S11. Results of the beta-regression with the proportion of disturbed forest corresponding to highest mixture diversity as a response variable.

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