











## RESEARCH ARTICLE OPEN ACCESS

# Structural and Compositional Disturbance Legacies Mediate the Resistance of European Forests to Repeated Disturbances

Niko Kulha<sup>1,2</sup>  | Georges Kunstler<sup>3</sup>  | Björn Reineking<sup>3</sup>  | Mikko Peltoniemi<sup>1</sup>  | Juha Honkaniemi<sup>1</sup>  | Kari T. Korhonen<sup>4</sup>  | Paloma Ruiz-Benito<sup>5</sup>  | Miguel A. Zavala<sup>5</sup>  | Pedro Rebollo<sup>5,6</sup>  | Julien Barrere<sup>3,7</sup> 

<sup>1</sup>Natural Resources Institute Finland (Luke), Helsinki, Finland | <sup>2</sup>Department of Biology, Aarhus University, Aarhus, Denmark | <sup>3</sup>Univ. Grenoble Alpes, INRAE, LESSEM, St-Martin-d'Hères, France | <sup>4</sup>Natural Resources Institute Finland (Luke), Joensuu, Finland | <sup>5</sup>Grupo de Ecología y Restauración Forestal, Departamento de Ciencias de la Vida, Universidad de Alcalá, Madrid, Spain | <sup>6</sup>Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Madrid, Spain | <sup>7</sup>INRAE, Aix Marseille Université, UR RECOVER, Aix-en-Provence, France

**Correspondence:** Niko Kulha ([niko.kulha@gmail.com](mailto:niko.kulha@gmail.com))

**Received:** 13 March 2025 | **Revised:** 9 July 2025 | **Accepted:** 30 July 2025

**Handling Editor:** Jonathan Belmaker

**Funding:** This work was supported by the BiodivClim ERA-Net Cofund (joint BiodivERSA Call on 'Biodiversity and Climate Change', 2019–2020) with national co-funding through ANR (France, project ANR20-EBI5-0005-03), Research Council of Finland (decision no. 344722), and Federal Ministry of Education and Research (Germany, grant no. 16LC2021A). This study has also received co-funding from the European Union's Horizon 2020 Research and Innovation Program under Grant Agreement 101000574. N.K. was also supported by the Osk. Huttunen Foundation. J.H. was supported by the Research Council of Finland (decision no. 342569). P.R.B., M.A.Z. and P.R. are supported by the Science and Innovation Ministry, AEI (Agencia Estatal de Investigación) (subproject LARGE, No. PID2021-123675OB-C41) and by grant VERDAT; MITECO, Organismo Autónomo de Parques Nacionales, Ref. 2794/2021. P.R.B. was also supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010).

**Keywords:** disturbance dynamics | disturbance regime | forest structure | national forest inventory | resistance | sensitivity | species diversity disturbance

## ABSTRACT

**Aim:** Climate change is altering forest disturbance regimes across Europe. Structural and species diversity are generally thought to enhance disturbance resistance. However, how disturbances affect stand structure and tree species diversity remains untested across broad spatial gradients and for multiple disturbance agents. Furthermore, determining how disturbance-induced changes affect resistance to subsequent disturbances is critical for understanding forest dynamics in the face of global change.

**Location:** The forests of Finland, France and Spain.

**Time Period:** 1986–2020 CE.

**Major Taxa Studied:** Trees.

**Methods:** We examined the effects of tree size and tree species diversity on resistance to fire, wind, biotic and snow disturbances using a National Forest Inventory dataset of 4827 disturbed plots. We quantified disturbance resistance as the tree mortality response to different severity disturbances. We modelled the immediate disturbance-driven changes in structural and tree species diversity, and predicted how these changes affect resistance to subsequent disturbances.

**Results:** High structural diversity increased stand resistance to snow disturbance, and high species diversity decreased resistance to fire. Severe disturbances consistently decreased structural and species diversity across all disturbance agents. However, both diversity metrics increased after low severity snow disturbances, and structural diversity increased after low severity biotic disturbance. Resistance to subsequent disturbance increased after low severity fire and low to moderate severity wind

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

disturbances. Biotic and snow disturbance had the opposite effect, with moderate severity disturbances decreasing resistance to subsequent disturbance more than low severity disturbances.

**Main Conclusions:** Structural and species diversity had little effect on plot-level disturbance resistance. Severe disturbances consistently decreased structural and species diversity, while low to moderate severity disturbances can increase these diversities. Resistance to subsequent disturbance is contrasted between disturbance agents and disturbance severity. Increasing disturbance severity may decrease structural and species diversity in future forests.

## 1 | Introduction

Disturbance regimes are changing across Europe. Evidence of these changes includes an increased prevalence of specific disturbance agents (e.g., wind; Senf and Seidl 2021b), changing geographic distributions of disturbance agents (Dupuy et al. 2020), and more frequent recurrence of disturbances (Senf and Seidl 2021a). Consequently, tree mortality is increasing (Patacca et al. 2022; Senf et al. 2018). These changes have the potential to alter forest structure (Haber et al. 2020) and compromise ecosystem functionality (Messier et al. 2022) and the provisioning of ecosystem services (Lecina-Diaz et al. 2024). This calls into question the ability of forests to remain unchanged, that is, to be resistant (Grimm and Wissel 1997), under the changing disturbance regimes and highlights the need to improve our understanding of disturbance resistance.

Research on forest disturbance resistance consistently shows that disturbance intensity—such as wind speed (Valta et al. 2019) or the amount of energy released in a fire (Keeley 2009)—has an overriding effect on disturbance resistance, with high-intensity disturbances causing the most tree mortality (Halpern 1988). Besides disturbance intensity, factors such as stocking, species composition and tree size influence disturbance resistance, with varying effects between disturbance agents (Schmitt et al. 2020; Siipilehto et al. 2020). For instance, large trees may be fire resistant due to thick bark (Michaletz and Johnson 2007; Trouvé et al. 2021), but are more susceptible to wind than small trees (Gardiner et al. 2010). In studies of algal or grassland communities, disturbance resistance has also been attributed to ecosystem complexity (Pimm 1984) and species diversity (Allison 2004; Isbell et al. 2015), but whether this applies to forests is unclear. Forest ecosystem complexity—interpreted here as structural diversity—may influence disturbance resistance by, for example, mediating how wind transmits through and between stands (Kulha et al. 2024; Mitchell 2013), modifying snow accumulation through canopy stratification (Fahey et al. 2020), or influencing fire spread through fuel continuity (Niklasson and Granström 2000; Kafka et al. 2001). Species diversity—interpreted here as tree species diversity—may influence disturbance resistance by increasing the complementarity of ecological traits and thus niche differentiation among species, which affects the stands mean disturbance resistance (the insurance hypothesis; Yachi and Loreau 1999). Species diversity may also influence disturbance resistance through the sampling effect (Huston 1997; Tilman 1997), whereby a greater number of species increases the likelihood that at least some species in a stand will be resistant (Tilman 2001). Due to the large number of disturbed stands required to empirically test

these theories, it remains largely unknown whether structural and species diversity uniformly increase forest resistance to different disturbance agents across broad geographic gradients.

As part of changing disturbance regimes, the increasing disturbance frequency (Turner and Seidl 2023) suggests that disturbances are recurring faster than the time required for forests to recover to a pre-disturbance state (Seidl and Turner 2022). Thus, the ability of a stand to resist disturbance depends on the structural and compositional legacies of the previous disturbance. Different disturbances leave different legacies, depending, for example, on disturbance agent, disturbance severity and pre-disturbance stand characteristics (Alfaro-Sánchez et al. 2024; Atkins et al. 2020; Gough et al. 2022). At the stand level, high-severity disturbances typically reduce structural (Ankori-Karlinsky et al. 2024; Bače et al. 2015) and species diversity (Foster 1988; Halpin and Lorimer 2016; Reyes et al. 2010) simply because these disturbances remove most trees in the stand. In contrast, disturbances of low to moderate severity (i.e., partial disturbances) can leave highly variable structural and compositional legacies (Fahey et al. 2020; Stuart-Haëntjens et al. 2015; Woods 2004) that strongly alter the successional trajectory of the disturbed stand (Braziunas et al. 2018; Gauthier et al. 2010; Kulha, Ahokas, et al. 2023). The different structural and compositional legacies of disturbances may lead to the development of stands with new ecological properties (emergent properties *sensu* Mitchell et al. 2023), for example, with respect to their adaptation to the prevailing disturbance regime (Bače et al. 2015). To date, different structural and compositional legacies of disturbances remain understudied over broad scales and for multiple disturbance agents (Atkins et al. 2020). This limits our understanding of how increasingly frequent disturbances change forest structure and tree species diversity.

The structural and compositional disturbance legacies influence the ability of stands to resist subsequent disturbances (Buma 2015; Cannon et al. 2017; Simard et al. 2011). In many cases, the occurrence of a disturbance reduces stand-level resistance to a subsequent disturbance. For example, wind disturbance may initiate a bark beetle outbreak (Hlásny et al. 2021) or promote fire intensity (Cannon et al. 2019) by providing breeding material or increasing flammability and fuel load, respectively. However, this is not necessarily the case for recurrent disturbances (i.e., the same disturbance occurring again), as the trees remaining after the initial disturbance event are theoretically the most resistant to the recurrence of the same disturbance. For example, a storm that removes only the top canopy trees may homogenise forest structure and increase stand resistance to high winds (Mitchell 2013;

Stovall et al. 2019). Similarly, fire can reduce susceptibility to a subsequent fire by reducing fuel load and removing non-fire-adapted species (Buma et al. 2020). However, it remains untested whether these buffering effects of disturbance recurrence occur uniformly for different disturbance agents and disturbance severities.

In this study, we used National Forest Inventory data and regression models to investigate the stand-level relationship between structural and species diversity and disturbance resistance separately for fire, wind, biotic and snow disturbance along a latitudinal gradient from the Mediterranean to the Arctic. We examined how stand structure and species diversity change with disturbance severity, which we defined as the proportion of basal area per hectare of trees that died due to a disturbance, and modelled the associated changes in resistance to recurrent disturbance. Specifically, we asked: (1) How does structural and tree species diversity influence resistance to different disturbance agents? (2) How do different disturbance agents and severities change structural and tree species diversity? and (3) How does the occurrence of disturbance change resistance to subsequent disturbance?

## 2 | Materials and Methods

### 2.1 | National Forest Inventory Data

We used National Forest Inventory (NFI) data from three European countries, Finland, France and Spain, to examine plot-level disturbance resistance (Table 1). We chose data from these three countries because they report observations of the major disturbance agents in Europe from at least two inventories and together cover a broad climatic gradient across the continent. In each country, the NFI is based on circular plots with different sampling radii depending on tree size between the countries (Table 1). Tree-level information includes data such as tree diameter at breast height (hereafter DBH), species and status (live, dead, or harvested). The time interval between two inventories is systematically 5 years in France, 5 years on average in Finland and 10 years on average in Spain. Measurements were made between 2010 and 2020 in France, 2014 and 2020 in Finland and 1986 and 2008 in Spain.

We only considered plots that were measured twice to quantify true mortality events. Because we were interested in the effect of structural and tree species diversity on disturbance resistance, we excluded plots with fewer than four trees as they had low structural and species diversity in our data (Figure S1). We selected plots that had been disturbed by either fire, wind, biotic agents, or snow between two censuses. We considered a plot disturbed if a disturbance was recorded in the data and at least one tree on the plot died between the censuses. Unlike fire and wind, which were reported in all three countries, we could only use data from Spain and Finland for biotic and snow, as these two disturbances were not reported in separate categories in France. In our data, biotic disturbances are caused by multiple agents. In Finland, these agents were pathogens or fungi (78.0%), insects (16.5%) and vertebrates (5.5%), mostly beavers. In Spain, biotic disturbances were caused by insects (36.4%), pathogens or fungi (31.6%), mistletoe (31.0%) and vertebrates (1.0%).

We removed all trees with a DBH of  $< 10$  cm at the first census to harmonise the datasets, and retained only trees that were alive at the time of the first census for further analysis. Most NFI-based studies of natural tree mortality exclude plots that are harvested during the study period because it is not known whether the trees were dead or alive at the time of harvest and/or because harvesting could affect the natural mortality rate (Kulha, Honkaniemi, et al. 2023; Kunstler et al. 2021). However, because salvage logging is extremely common after disturbances (Leverkus et al. 2018; Suvanto et al. 2025) and is even legally required in some countries such as Finland (Finnish Damage Prevention Act 1087/2013), such a criterion would exclude many disturbance events and could bias the data towards stands of low economic value and/or towards stands affected by low severity disturbances. For these reasons, we chose to keep the disturbed plots that had been harvested and assumed that the harvests were salvage loggings (i.e., all the trees that died between censuses were killed by the disturbance). In our data, harvested plots accounted for 7% of the total number of plots and 6% of the total basal area examined. Using these criteria, we examined a total of 479, 560 and 3788 disturbed plots in Finland, France and Spain, respectively (Table 1).

### 2.2 | Structural and Tree Species Diversity

We quantified plot-level structural diversity for diameter at breast height (DBH) using the Gini coefficient (hereafter Gini), a common diversity index that has been shown to be better at examining size inequality in tree data than other indices such as height diversity metrics (Valbuena et al. 2012; Valbuena 2015). The Gini is usually conceptualised as the difference between a diagonal line showing absolute equality in a cumulative percentage of a population attribute, in our case tree DBH, and the observed cumulative percentage of the same attribute, represented by a Lorenz curve. The larger the area between the two lines, the greater the inequality of the population attribute. See Dorfman (1979) for a quantification of the coefficient. The Gini can range from zero (all individuals of equal size) to a theoretical maximum of one, which represents perfect inequality. In our data, the Gini ranged from 0.010 to 0.448. In calculating the Gini, we weighted each tree by the number of trees it represents per hectare to account for differences in sampling design between countries.

We calculated tree species diversity at the plot level using the Shannon Diversity Index (hereafter Shannon), a long-established method for characterising species diversity in a community and that considers the relative abundance of species in the community (Hill 1973). The index is widely used in ecology to quantify species diversity (Spellerberg and Fedor 2003) and is particularly useful when estimating species diversity using NFI data (Borghi et al. 2024). Because NFI plots often contain few species, simpler metrics such as richness would poorly distinguish these plots. Thus, accounting for relative abundance, which is accurately estimated in NFI data, is key to capturing differences in species evenness between plots. We used the summed basal area per hectare of each species as the abundance metric in the Shannon calculation. To compare pre- and post-disturbance species diversity, we exponentiated the Shannon values following Jost (2006).

**TABLE 1** | Summary of the National Forest Inventory data used in this study.

	<b>Finland</b>	<b>France</b>	<b>Spain</b>
Sampling design	Nested circular subplots with fixed or varying radius. The fixed plot radii are 5.64 and 9 m. The DBH thresholds are 4.5 and 9.5 cm, respectively	Nested circular subplots with radii of 6, 9 and 15 m. Trees with a minimum DBH of 7.5, 22.5 and 37.5 cm are measured on the subplots, respectively	Nested circular subplots with radii of 5, 10, 15 and 25 m. Trees with a minimum DBH of 7.5 cm, 12.5 cm, 22.5 cm and 42.5 cm and 130 cm of height are measured on the subplots, respectively
Number of observations			
Total number of disturbed plots used in this study	479	560	3788
Number of fire-disturbed plots	0	20	883
Number of plots with biotic disturbance	150	—	2297
Number of wind-disturbed plots	87	540	404
Number of snow-disturbed plots	242	—	204
More information on the NFI	Natural Resources Institute Finland <a href="https://www.luke.fi/fi/seurannat/valta">https://www.luke.fi/fi/seurannat/valta</a> <a href="https://www.luke.fi/fi/seurannat/valta">https://www.luke.fi/fi/seurannat/valta</a> kunnan-metsien-inventointi-vmi	Institut national de l'information géographique et forestière <a href="https://www.ign.fr/institut/nos-domaines-dintervention/foret">https://www.ign.fr/institut/nos-domaines-dintervention/foret</a>	Inventario Forestal Español: <a href="https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html">https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html</a>

This true diversity, or the effective number of types, refers to the number of equally abundant types needed for the average proportional abundance of the types to equal that observed in the dataset of interest (where not all types are necessarily equally abundant) (Hill 1973).

### 2.3 | Control Covariates

To account for the effect of stocking and tree size on disturbance resistance, we calculated the stand basal area ( $\text{m}^2 \text{ha}$ ) and quantified mean *DBH* in cm, weighted by the number of trees a tree represents per hectare.

We classified the plots as either coniferous ( $C=0$ ) if  $\geq 50\%$  of the basal area of the plot was coniferous at the time of the census, or otherwise broadleaved ( $C=1$ ) to account for the difference in disturbance resistance between coniferous and broadleaved species. We used this two-level categorical variable to represent dominance type instead of the proportion of conifers or the classification as coniferous, broadleaved, or mixed because of the covariance between the Shannon and these two dominance variables (Pearson's correlation between the Shannon and the proportion of conifers ranged  $-0.52$  to  $-0.24$ , depending on the disturbance agent) (Figures S2 and S3).

Disturbance intensity is one of the main drivers of disturbance-induced tree mortality (Miquelajauregui et al. 2016; Greenwood et al. 2017). However, disturbance intensity is rarely considered in field studies because it is difficult to measure directly and accurately at the time of disturbance. Disturbance intensity is also difficult to quantify retrospectively, especially for datasets with a wide geographic gradient, such as NFI, if the exact time of disturbance occurrence is unknown. Nevertheless, we attempted to control for the effects of disturbance intensity by calculating climate indices related to fire, wind and snow disturbance intensity between inventory measurements. For fire, we extracted the daily Fire Weather Index (FWI)—an index related to the meteorological conditions favourable for fire ignition, spread and persistence (Vitolo et al. 2020)—and calculated the 97.5% quantile over the entire period between the two censuses for each plot. For wind, we took the maximum monthly wind speed at 10 m height between the two censuses at each plot. For snow, we extracted the monthly snow water equivalent (SWE)—that is, the resulting water column if a snowpack were to melt in place (Takala et al. 2011)—and calculated the maximum monthly value between the two censuses for each plot. These three climate indices were extracted from the Climate Data Store of the Copernicus Climate Change Service and Climate Data Store (2019) (Muñoz Sabater 2019). We were unable to account for the intensity of biotic disturbances due to a lack of appropriate data. We recognise that disturbance intensity, such as wind gust speed (Laapas et al. 2023), can show considerable fine-scale variability that is difficult to capture using coarse-grained continental-scale data. However, since fine-scale disturbance intensity data of consistent quality are not available throughout our study area, we consider our approach to control for disturbance intensity to be the best possible compromise.

We calculated community-weighted means (with basal area per hectare as the abundance metric) of the functional traits most

directly related to the resistance to each disturbance agent to control for interspecific differences in disturbance resistance, drawing from the results in Barrere et al. (2023). Accordingly, we used bark thickness for fire, wood density for wind and leaf nitrogen content for biotic disturbance. We did not quantify community-weighted means for snow because no single species-level trait was significantly related to resistance to snow disturbance (Barrere et al. 2023). We calculated bark thickness directly from the NFI data and extracted wood density from the wood density database (Chave et al. 2009) and leaf nitrogen content from the TRY database (Kattge et al. 2011). For full details on the calculation of these functional composition variables at species level, see Barrere et al. (2023) and the Supporting Information S1 therein.

## 2.4 | Statistical Analyses

### 2.4.1 | The Effect of Structural and Tree Species Diversity on Disturbance Resistance

To answer our first research question on how structural and tree species diversity influence disturbance resistance, we calculated the ratio of basal area (BA) per ha of trees that survived the disturbance to the pre-disturbance basal area, hereafter referred to as disturbance resistance and denoted with  $R$ . We modelled the relationship between  $R$  and plot-level structural and species diversity with beta regression models with a logit link function separately for fire, wind, biotic and snow disturbance because we expected the relationship between disturbance resistance and structural and species diversity to vary by disturbance. In each model, the main covariates were two diversity metrics: structural diversity, quantified by the Gini coefficient ( $G$ ) and tree species diversity, measured by the Shannon diversity index ( $H$ ). We initially included functional diversity ( $FD$ ) (see its quantification in Supporting Information S1, Figures S4 and S5) in the models, but the correlation between  $H$  and  $FD$  was too high to keep both variables in the same model (Pearson's  $r$  0.71–0.86, depending on the disturbance; Figure S2), and the models with  $FD$  were rejected based on AIC comparison (Table S1). In addition to structural and species diversity, we included the control covariates described in the previous section—that is, dominance type ( $DT$ ) (coniferous or broadleaved), total BA, mean *DBH*, community weighted means ( $C$ ) of bark thickness (fire), leaf nitrogen mass (biotic) or wood density (wind), and the disturbance intensity indices ( $I$ ) (fire weather index, max wind speed or snow water equivalent) as explanatory variables in the model, and a country-specific intercept. We also included an interaction between  $BA$  and  $DT$  in the model when significant. Accordingly, the models had the form:

$$\text{Logit}(R_{ip}) = \alpha_{0,i,\text{country}} + \alpha_{1,i}DT_p + \alpha_{2,i}BA_p + \alpha_{3,i}DBH_p + \alpha_{4,i}C_p + \alpha_{5,i}I_p + \alpha_{6,i}G_p + \alpha_{7,i}H_p + \alpha_{8,i}BA_p \times DT_p + \varepsilon + \ln(t_{xp}) \quad (1)$$

where,  $\text{Logit}(R_{ip})$  is the logit-transformed disturbance resistance  $i$  on plot  $p$ .  $\alpha_{0-8,i}$  are coefficients specific to the disturbance  $i$ , and  $\ln(t_{xp})$  is an offset that we used to control for different census lengths between the two inventories.

For all disturbances except for fire, we observed mostly low severity events, potentially leading to a disproportionate

influence of low severity disturbances on the model parameters (Figure S6). To account for this uneven distribution, we divided the data for each disturbance agent into 10 fixed-interval classes of disturbance severity (proportions of basal area of dead trees ranging from 0–0.1 to 0.9–1). Then, we assigned each observation a weight equal to the ratio of the average number of observations across the 10 classes to the number of observations in that class so that disturbance severity distribution does not bias the results. We also tested whether the Pearson residuals of the models were related to the average climate on the plot and looked for other patterns in the residuals. The residuals were independent of climate (Figure S7) but indicated that the models did not capture the high extremes of the observed responses well (Figure S8), which is not unexpected given the stochastic nature of disturbance mortality. We also fitted country-specific resistance models for each agent with sufficient data to examine whether the country-specific parameter estimates were similar to those of the global model. To examine the effect of salvage logging on our results, we also fitted the resistance models using data only from non-harvested plots. We fitted the beta regression models for response data containing boundary observations at 1 using the *betareg* package (Kosmidis and Zeileis 2025) in R version 4.4.3 (R Core Team 2024).

#### 2.4.2 | The Effect of Disturbance on Structural and Species Diversity

To examine how disturbances change plot-level structural and species diversity, our second research question, we calculated an index of change (IC) in structural diversity ( $IC(Gini)$ ) and in species diversity ( $IC(Shannon)$ ) as the log-ratio of post-disturbance value divided by pre-disturbance value of each diversity metric (Gini coefficient and exponential of Shannon index). Log-ratio values above 0 indicate an increase in tree species or structural diversity after disturbance; values below 0 indicate a decrease, and a value of 0 indicates no change. We fitted agent-specific models (i.e., one model for each disturbance: fire, biotic, wind or snow) using GLMs with Tweedie error distributions and log link functions:

$$\log\left(\frac{G_{a,p}}{G_{b,p}}\right) = \beta_{1,i}S_p + \beta_{2,i}S_p^2 + \epsilon \quad (2)$$

$$\log\left(\frac{\exp(H_{a,p})}{\exp(H_{b,p})}\right) = \gamma_{1,i}S_p + \gamma_{2,i}S_p^2 + \epsilon \quad (3)$$

where,  $G_{b,p}$  and  $H_{b,p}$  are Gini and Shannon before and  $G_{a,p}$  and  $H_{a,p}$  after the disturbance on plot  $p$ , respectively.  $S_p$  is the disturbance severity (i.e., the proportion of basal area per hectare of trees that died due to a disturbance) on plot  $p$ , and  $\beta_{1-2}$  and  $\gamma_{1-2}$  are coefficients specific to disturbance agent  $i$ . We included a quadratic effect of disturbance severity in the model to allow for a nonlinear relationship and, similar to the model shown in Equation (1), used the ratio of the average number of observations across the 10 disturbance severity classes to the number of observations in the class of the observation as statistical weight in the models to account for the skewness of the data (Figure S9). Since a disturbance that causes no mortality cannot

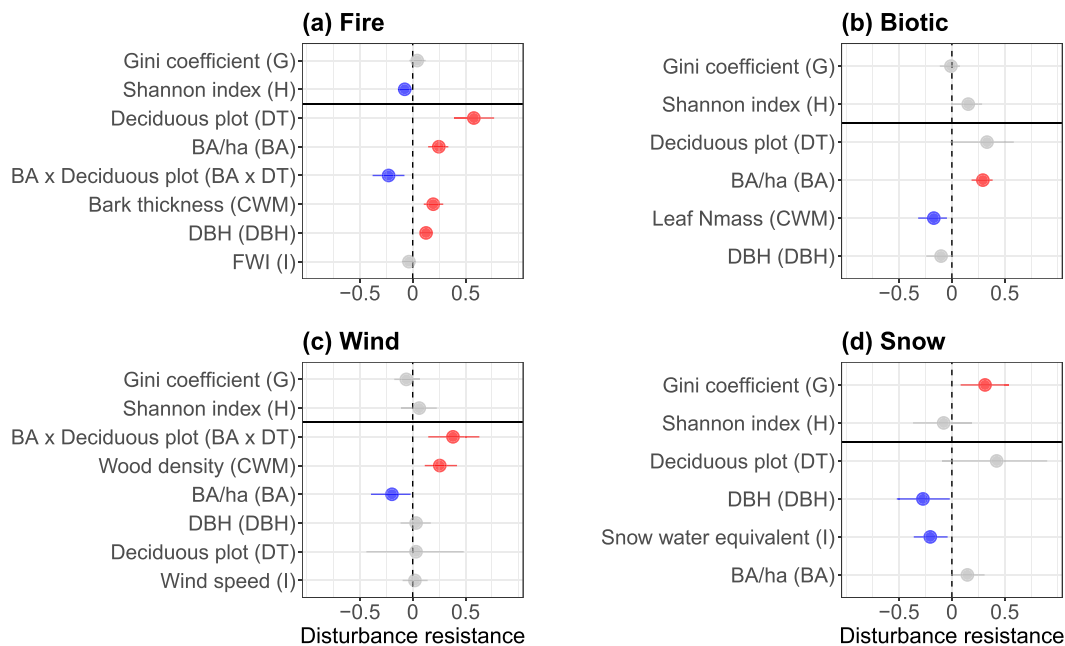
change structural or species diversity, we forced the model intercepts to zero for a disturbance severity of zero. We excluded plots that were initially monospecific from the tree species diversity model (Equation 3) because the species diversity of these plots could not change between inventories in our data where ingrowth were not counted. For this reason, our results depict changes in diversity immediately after disturbance. In cases where the effects of  $S$  and  $S^2$  were not significant, we fitted one model with only  $S$  and one model with only  $S^2$ ; we selected the most parsimonious model based on AIC (Table S2). To verify that our results were robust to the method of analysis, we also fitted alternative models using the log of the diversity metric (Gini or exponentiated Shannon) after disturbance as the response variable and the diversity metric before disturbance as an offset. We fit these models using the *statmod* package (Dunn and Smyth 2018) in R version 4.4.3 (R Core Team 2024).

#### 2.4.3 | The Effect of Disturbance on Resistance to Subsequent Disturbance Through Structural and Compositional Legacies

To study how disturbances affect resistance to subsequent disturbance, our third research question, we used the predictions of the models presented in Equation (1) to quantify disturbance resistance to each disturbance agent  $i$  based on the trees alive at the first inventory (initial resistance to disturbance  $i$ ,  $R_i$ ) and at the second inventory (resistance to disturbance  $i$  after disturbance  $j$ ,  $R'_i$ ). Using these two predictions, we calculated an index of change for disturbance resistance (IRC) in plot  $p$  following a disturbance  $i$  as:

$$IRC_{ijp} = 100 \times (R'_i - R_i) \div R_i \quad (4)$$

where,  $IRC_{ijp}$  is the percentage of change in resistance to disturbance  $i$  on plot  $p$  caused by the occurrence of low (1%–25% of initial basal area dead after the disturbance) to moderate (26%–50% of initial basal area dead after disturbance) severity disturbance  $j$ . For example, if a plot disturbed by fire (disturbance  $i$ ) experienced a subsequent fire (disturbance  $j$ ), an  $IRC_{ijp}$  value of 20 means that fire occurrence increased resistance to fire by 20%. Similarly, an  $IRC_{ijp}$  value of –20 means that fire decreased the plot's resistance to fire by 20%. For simplicity, we only examined the change in disturbance resistance to a repetition of the same disturbance. Because we expected resistance to a subsequent disturbance to depend on the severity of the disturbance, we examined the change in disturbance resistance separately after a low and a moderate severity disturbance. We used a one-sample  $t$ -test to test whether the change in disturbance resistance before and after the disturbance was significantly different from zero. We did not include high severity disturbances (51%–100% of initial basal area dead after disturbance) in this analysis because in these plots the post-disturbance plot BA was mostly outside the range of the data used to fit the disturbance resistance models presented in Equation (1), and because the number of plots with high severity disturbances was low (3.2% of the whole data) compared to disturbances of low to moderate severity (Figure S10).



**FIGURE 1** | Parameter estimates for structural and species diversity and the control covariates in the regression models with disturbance resistance, quantified as the plot-level ratio of basal area of trees that survived a disturbance ( $R$ ), as a response variable for fire (a), biotic (b), wind (c) and snow disturbance (d). Estimates are from the models fitted with scaled and centred covariates. Points are model parameter estimates and the error bars are bootstrapped 95% confidence intervals for the estimates. Red dots indicate a significant increase, and blue dots indicate a significant decrease in disturbance resistance at the 0.05 level. Light grey dots are non-significant covariates. FWI and SWE are fire weather index and snow water equivalent, respectively. The symbols in parentheses refer to those used in Equation (1). Numerical model parameter estimates are given in Table S3.

### 3 | Results

#### 3.1 | Components of Disturbance Resistance

Disturbance resistance was generally not related to structural or species diversity (see parameter estimates of Gini coefficient and Shannon index in Figure 1, Table S3). For structural diversity, the only exception we found was resistance to snow disturbance, which increased with increasing structural diversity (Figure 1d). For snow disturbance, structural diversity also had the highest relative contribution in increasing disturbance resistance among all statistically significant covariates (Figure 1d, Table S3). For species diversity, the only exception we found was for fire resistance, which decreased with increasing species diversity (Figure 1a).

Dominance type, that is, whether the plot was dominated by broadleaved or coniferous species, had the highest relative contribution to fire resistance and significantly interacted with plot basal area (Figure 1a). Plots dominated by broadleaved trees and with a basal area of approximately  $>40\text{ m}^2/\text{ha}$  were less resistant to fire than similar coniferous plots, but this was reversed between dominance types for plots with a basal area  $<40\text{ m}^2/\text{ha}$  (Figure 1a, Figure S11a). Plots with high basal area were also more resistant to biotic disturbances (Figure 1b), while plots with low basal area were more resistant to wind (Figure 1c), but only in coniferous-dominated plots (Figure S11b). In plots dominated by broadleaves, wind resistance increased with increasing basal area (Figure 1c, Figure S11b). However, dominance type did directly affect wind disturbance resistance, possibly because

we did not categorise admixtures separately due to collinearity with species diversity.

Higher bark thickness (Figure 1a) and wood density (Figure 1c) increased resistance to fire and wind disturbance, respectively, while the resistance to biotic disturbance decreased with increasing mean leaf nitrogen mass (Figure 1b). Plots with high mean DBH had higher resistance to fire (Figure 1a) but lower resistance to snow disturbances (Figure 1d). Resistance to snow disturbance decreased with increasing snow water equivalent, the variable controlling for snow disturbance intensity (Figure 1d). The other climate indices related to disturbance intensity (fire weather index and maximum wind speed) had no significant effect on resistance to fire or wind, respectively (Figure 1).

In general, the parameter estimates of the global models were consistent with those of the country-specific models, and with those of the models fitted only to data from non-harvested plots (Tables S3 and S4).

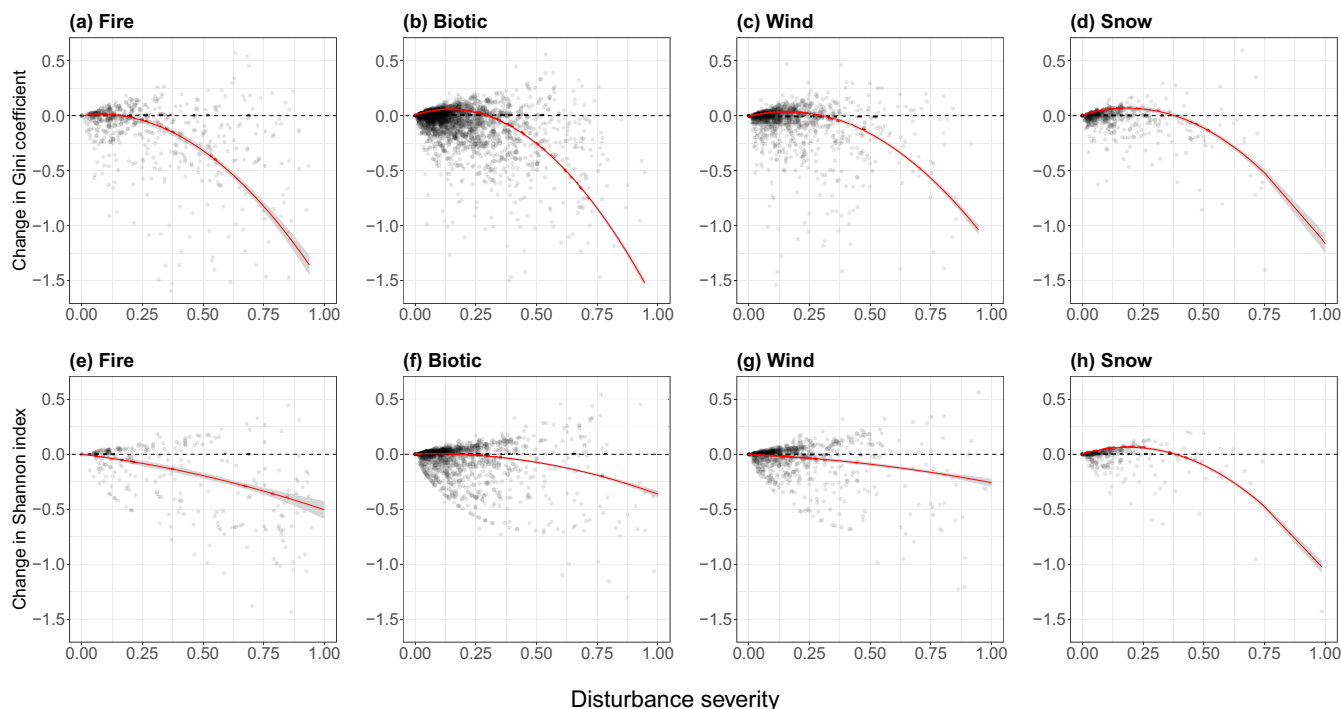
#### 3.2 | Post-Disturbance Structural and Species Diversity

Post-disturbance structural and tree species diversity was typically lower than pre-disturbance structural and species diversity when disturbance severity exceeded 30% (i.e.,  $>30\%$  of plot basal area dead) (Figure 2a–d, Figure S12). However, biotic, wind and snow disturbances that reduced plot basal area by  $<30\%$  increased structural diversity (Figure 2b–d).

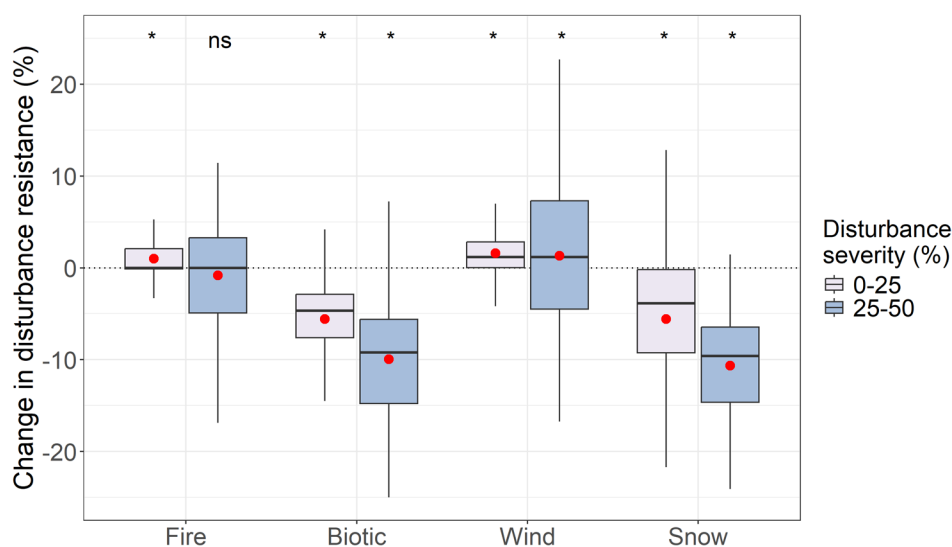
Post-disturbance tree species diversity was consistently lower than pre-disturbance tree species diversity independent of disturbance intensity except for snow disturbance, where disturbance with severity less than approximately 35% increased tree species diversity (Figure 2e–h). These results were consistent with the results of the model where we used the pre-disturbance diversity as an offset (Figure S13).

### 3.3 | The Effect of Disturbances on the Resistance to Subsequent Disturbances

The occurrence of a fire with a severity < 25% (i.e., < 25% of plot basal area dead) or a wind disturbance with a severity < 50% increased the plot-level resistance to a subsequent disturbance by the same agent ( $p < 0.01$ ) (Figure 3). On average, resistance



**FIGURE 2** | The predicted change in structural (a–d) and species diversity (e–h) as a function of relative disturbance severity for different disturbances. The lines are the predicted change in structural diversity (a–d) or species diversity (e–h), the points are the original data, and the shaded areas are the 95% confidence intervals of the predictions. Values above 0 on the y-axis indicate an increase in structural or species diversity; values below 0 indicate a decrease, and a value of 0 indicates no change. The numerical model parameter estimates are given in Table S5. Note that the structural diversity model predictions are log-transformed to be consistent with the species diversity model predictions.



**FIGURE 3** | Change in disturbance resistance after the occurrence of a low (0%–25%) or moderate severity (25%–50%) disturbance against disturbance by the same agent. Positive values indicate a proportional increase in disturbance resistance and vice versa. Asterisks indicate when the mean (red dots) is significantly different from zero at the 0.05 level according to the one-sample  $t$ -test, and ns indicates a non-significant difference from zero.

to subsequent disturbance increased by 1.0% after a fire with a severity below 25%, 1.6% after a wind disturbance with a severity below 25%, and 1.3% after a wind disturbance with severity between 25% and 50% (Figure 3). Resistance to subsequent biotic disturbance decreased by 5.8% and 10.9% after a biotic disturbance with severity below 25% and between 25% and 50%, respectively ( $p < 0.01$ ). Resistance to subsequent snow disturbance decreased by 7.1% and by 13.7% after a snow disturbance with severity below 25% and with severity between 25% and 50%, respectively ( $p < 0.01$ ).

## 4 | Discussion

### 4.1 | Structural and Species Diversity Are Weakly Related to Disturbance Resistance

Our results indicate an overall poor correlation between stand resistance to disturbance and structural and species diversity. However, we identified two significant relationships: structural diversity improved resistance to snow disturbance, and high species diversity was associated with lower resistance to fire. In contrast to the other disturbances we studied, snow (and ice) is a top-down disturbance that affects canopies from above (Atkins et al. 2020), causing mortality particularly among trees with exposed crowns that collect the highest snow loads (Weeks et al. 2009; Fahey et al. 2020; Suvanto et al. 2020). Stands with high tree size variability (and thus high structural diversity in our analysis) typically have canopies in multiple layers (Georgi et al. 2022). In such stands, the effects of a top-down disturbance are greatest in the upper canopy layers, thereby reducing the severity of disturbance at the stand level (Nykänen et al. 1997). The negative correlation between species diversity and resistance to fire is consistent with an analysis of a 20-year time series of the Spanish NFI (Peris-Llopis et al. 2024). Increasing species diversity may reduce fire resistance through what can be thought of as the inverse of the sampling effect: the most diverse stands are most likely to contain species with mixed fire-adaptation strategies. This may favour the development of severe fires and thereby increase tree mortality (Peris-Llopis et al. 2024; Stevens et al. 2020), a mechanism that is similar to associational susceptibility in biotic disturbances (Jactel et al. 2017). In contrast, tree mortality from fire can remain low in a monoculture of fire-resistant species (González et al. 2007).

Contrary to expectations, we found no evidence that structural diversity increases the wind resistance of a stand, as shown in previous studies (Hanewinkel et al. 2014; Pukkala et al. 2016). Structural diversity may increase wind resistance because, for example, wind speeds can remain high and detrimental to trees within a uniformly sized stand (Morimoto et al. 2019). That we found no evidence that structural diversity increases stand wind resistance may be because the plot size in our data (radii of circular plots between 5 and 25 m) is too small to capture the diversity effect, that we did not account for the effect of stand neighbourhood on disturbance occurrence (Kulha et al. 2024), and/or that the effect is overwhelmed by the other numerous tree- and stand-level factors that contribute to wind resistance (Gardiner et al. 2010).

While several studies across forest biomes have suggested a positive effect of species diversity on resistance to biotic disturbance (Jactel et al. 2021; Jactel and Brockerhoff 2007 and references therein), such a dependence was not significant in our data. This may partly result from the fact that biotic disturbance in our data consists of disturbance by a broad group of agents, including fungi, pathogens and phytophagous and xylophagous insects (Aarnio et al. 2024), which may blur the relationship between species diversity and resistance. For example, the buffering effect of species diversity against insect disturbance is manifested mainly for host-specialist insect herbivores (Jactel et al. 2021) but is less clear in the case of more generalist pests.

It is also evident that the lack of a significant relationship between structural and species diversity and disturbance resistance may be due to a correlation between diversity and disturbance intensity that we could not fully control for due to spatially and temporally coarse covariates that did not capture disturbance intensity at the time of disturbance occurrence with the precision relevant to our plot-level analysis (cf. Laapas et al. 2023), except in the case of snow disturbance. This may be particularly true for biotic disturbances, as pest damage has been shown to peak in the least diverse stands (Guyot et al. 2016). However, wind and fire disturbance intensity would be expected to be less correlated with species or structural diversity than biotic disturbance intensity. Thus, the lack of spatially and temporally precise data on disturbance intensity should not bias our estimates of the effect of diversity on disturbance resistance. Instead, the overall weak effects of diversity we observed likely indicate that structural and species diversity are poor predictors of forest resistance to disturbance.

In contrast to the weak effect of diversity metrics, we found that stand basal area, composition and mean functional traits had a strong effect on resistance to all disturbances. However, mean tree size decreased disturbance resistance to snow disturbance. This may seem counterintuitive as structural diversity increased resistance to snow disturbance in our results. In our data for snow disturbance, mean tree size and structural diversity were positively related only until the mean size (DBH) reached approximately 17 cm, explaining the contrasting effects (Figure S14). An individual-based study using the same NFI data that we used concluded that disturbance resistance of individual trees is strongly influenced by species traits (Barrere et al. 2023). Furthermore, a meta-analysis focused on northern European forests also showed that functional traits are among the most important contributors to general disturbance resistance (Felton et al. 2024). Our results are consistent with these recent studies, which together show that compositional effects, mostly expressed in the traits of species present in a plot, rather than plot-level diversity metrics, explain disturbance resistance at this scale.

### 4.2 | Moderate to Severe Disturbances Decrease Structural and Tree Species Diversity

Low to moderate severity disturbances increased structural diversity, while moderate to severe ones decreased it

immediately after the disturbance. This pattern was consistent for all disturbance agents except fire. Our observations are consistent with other studies showing that low to moderate severity disturbances can increase stand structural diversity (Choi et al. 2023; Fahey et al. 2020; Haber et al. 2020; Peterson 2019), while high severity disturbances typically decrease stand structural diversity (Sommerfeld et al. 2021). This further suggests that forest structural diversity may peak when intermediate severity disturbances are prevalent (Nagel et al. 2021), consistent with the intermediate disturbance hypothesis (IDH). IDH, originally theorised for species diversity, suggests that disturbances of intermediate severity maintain the species diversity in ecological communities by allowing the coexistence of both late and early successional species (Connell 1978). Our results suggest that IDH may also apply to the maintenance of forest structural diversity, for example in cases where a disturbance removes average-sized trees from a stand, thereby increasing tree size inequality. This also suggests that low- to moderate-severity disturbances are beneficial for biodiversity, which has been shown to generally increase with increasing forest structural diversity due to increased niche availability (Gao et al. 2014; Hekkala et al. 2023).

Our results showed that disturbances tend to reduce species diversity, especially when the disturbance is severe. However, snow disturbances with low to moderate severity increased species diversity. Tree species vary in their disturbance resistance (Barrere et al. 2023), which could theoretically lead to two different effects of disturbance on species diversity, depending on which tree species dominate. If disturbance-resistant species dominate a stand, disturbance would reduce its species diversity by removing the minority of sensitive species. Conversely, if disturbance-sensitive species dominate, disturbance would increase species diversity by reducing the proportion of dominant species. Our results clearly show that most disturbances reduce species diversity, probably by increasing the relative abundance of already dominant, disturbance-resistant species. However, it is interesting to note that low to moderate severity snow disturbance promoted species diversity, as predicted by the IDH (Connell 1978). Snow increased species diversity, probably because this disturbance particularly affects the canopy-forming species. In our data, snow disturbance is most common in the northern plots, which are often dominated by a single species. Therefore, snow disturbance particularly reduces the relative abundance of the dominant species. However, as disturbance severity increases, tree mortality occurs regardless of species disturbance resistance (Miquelajauregui et al. 2016). Thus, it is likely that high severity disturbances reduce species diversity (Viljur et al. 2022), which is consistent with our results.

The frequency of low severity disturbances, which increase structural diversity in our results, and high severity disturbances, which decrease structural and species diversity in our results, is changing across Europe (Patacca et al. 2022; Senf and Seidl 2021a). Existing projections suggest an increase in disturbance severity under the changing climate (Seidl et al. 2017, 2020). In this context, our results suggest that climate change poses an increased risk of diversity loss as species increasingly encounter disturbance regimes with which they have not

coevolved. Furthermore, temporal change in the disturbance severity distribution will likely be a key parameter to consider when predicting future changes in structural and species diversity in forest ecosystems.

### 4.3 | Disturbances Have Varying Effects on Resistance to Subsequent Disturbances

Stands affected by low (< 25% of plot basal area dead) to moderate (between 25% and 50% of plot basal area dead) severity wind and fire disturbances showed increased resistance to subsequent disturbances. In the context of intensifying disturbance regimes (Patacca et al. 2022; Senf and Seidl 2021a), this suggests that certain stands may become more resistant to repeated disturbance. In general, the structural and compositional legacies of disturbances influence the ability of stands to resist future disturbances (Buma 2015; Cannon et al. 2017). For example, the occurrence of fire can reduce fuel loads and remove fire-sensitive species, thereby increasing resistance to immediate reburn (Buma et al. 2020). While more severe fires could also reduce fuel loads, they might also kill non-fire-sensitive species, thereby offsetting the effect of increasing resistance to reburn (Miquelajauregui et al. 2016). Similar to fire, low- to moderate-severity wind disturbances are also selective in that they primarily kill the most sensitive trees, which are often the tallest exposed trees with the longest lever arms (Everham and Brokaw 1996) and/or trees that are weakened by fungi or pathogens (Lännenpää et al. 2008), potentially homogenising forest structure. Trees in stands with homogeneous structure may experience relatively less wind loading and thus have higher resistance to wind compared to stands with more heterogeneous structure (Mitchell 2013). Consistent with previous findings (Gardiner et al. 2010), we also observed that coniferous plots with high basal area were less resistant to wind than broad-leaved plots. Therefore, as disturbance reduces the total basal area of these plots, their resistance to subsequent wind disturbance increases.

Our results for biotic and snow disturbances showed that the occurrence of these disturbances decreased plot-level resistance to subsequent disturbances. These results contrast with previous studies that showed increased resistance to successive insect disturbances (Bouchard et al. 2006; Sommerfeld et al. 2021) and no change in resistance to subsequent ice storms, which are analogous to snow disturbances (Fahey et al. 2020). The occurrence of biotic disturbances by specialist agents should exert negative feedback on repeated disturbance due to changes in tree species composition and reduced host availability (Hart et al. 2015). However, because biotic disturbance in our data consists of disturbance by a broad group of agents, including both generalists and specialists, the effect of host reduction on disturbance resistance is difficult to disentangle. For snow, our results show that these disturbances reduced plot-level structural diversity, which was the most important covariate explaining resistance to snow disturbance. As a top-down disturbance, snow disturbance is particularly detrimental to the uppermost canopy layer (Atkins et al. 2020). In a stand with a multilayered canopy structure, snow disturbance exposes the subcanopy layers to the disturbance (Nykänen et al. 1997), thereby reducing the resistance of the stand to repeated snow disturbance.

## 5 | Conclusions

Our analysis of 4827 disturbed plots in three countries spanning a latitudinal gradient from the Mediterranean to the Arctic revealed some important general trends in the interplay between structural and species diversity and disturbance resistance in European forests. First, structural diversity is more important than tree species diversity for disturbance resistance, but in general structural and tree species diversity explain disturbance resistance at the plot level only weakly and only for some agents, with a stronger effect of species composition, stocking and functional traits. Second, severe disturbances reduce stand structural and tree species diversity regardless of the disturbance agent, but low to moderate disturbances can also increase structural and species diversity. Third, post-disturbance resistance to subsequent disturbances is contrasted among disturbance agents: low to moderate severity fire and wind disturbances increase resistance, whereas biotic and snow disturbances decrease resistance.

### Acknowledgements

We are grateful for the availability of open access data for the Spanish NFI in the MITECO (<https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html>), for the availability of open access data for the French NFI, and for all the help provided in data processing. We thank Ville Pietilä (Luke) for preprocessing the Finnish NFI data. This research is funded through the BiodivClim ERA-Net Cofund (joint BiodivERsA Call on 'Biodiversity and Climate Change', 2019–2020) with national co-funding through ANR (France, project ANR20-EBI5-0005-03), Research Council of Finland (decision no. 344722), and Federal Ministry of Education and Research (Germany, grant no. 16LC2021A). This study has also received co-funding from the European Union's Horizon 2020 Research and Innovation Program under Grant Agreement 101000574. N.K. was also supported by the Osk. Huttunen Foundation. J.H. was supported by the Research Council of Finland (decision no. 342569). P.R.B., M.A.Z. and P.R. are supported by the Science and Innovation Ministry, AEI (Agencia Estatal de Investigación) (subproject LARGE, No. PID2021-123675OB-C41) and by grant VERDAT; MITECO, Organismo Autónomo de Parques Nacionales, Ref. 2794/2021. P.R.B. was also supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010). Open access publishing facilitated by Luonnonvarakeskus, as part of the Wiley - FinELib agreement.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The code to reproduce the results of our study is available in Figshare with DOI: [10.6084/m9.figshare.29488217](https://doi.org/10.6084/m9.figshare.29488217). The Spanish and French NFI data are available from the official data portals, <https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible.html> for Spain and <https://inventaire-forestier.ign.fr/dataIFN/> for France. Due to data disclosure restrictions, the Finnish NFI data used in this study are not openly available. Inquiries about the Finnish NFI data should be directed to the Forest Inventory and Planning group at the Natural Resources Institute of Finland.

### References

Aarnio, L., J. Hantula, H. Henttonen, et al. 2024. *Metsätuhot Vuonna 2023 (34; Luonnonvara- ja Biotalous Tutkimus)*. Luonnonvarakeskus.

Alfaro-Sánchez, R., J. F. Johnstone, and J. L. Baltzer. 2024. "Low-Severity Fires in the Boreal Region: Reproductive Implications for Black Spruce Stands in Between Stand-Replacing Fire Events." *Annals of Botany* 135: mcae055. <https://doi.org/10.1093/aob/mcae055>.

Allison, G. 2004. "The Influence of Species Diversity and Stress Intensity on Community Resistance and Resilience." *Ecological Monographs* 74, no. 1: 117–134. <https://doi.org/10.1890/02-0681>.

Ankori-Karlinsky, R., J. Hall, L. Murphy, et al. 2024. "Chronic Winds Reduce Tropical Forest Structural Complexity Regardless of Climate, Topography, or Forest Age." *Ecosystems* 27: 479–491. <https://doi.org/10.1007/s10021-024-00900-5>.

Atkins, J. W., B. Bond-Lamberty, R. T. Fahey, et al. 2020. "Application of Multidimensional Structural Characterization to Detect and Describe Moderate Forest Disturbance." *Ecosphere* 11, no. 6: e03156. <https://doi.org/10.1002/ecs2.3156>.

Bače, R., M. Svoboda, P. Janda, et al. 2015. "Legacy of Pre-Disturbance Spatial Pattern Determines Early Structural Diversity Following Severe Disturbance in Montane Spruce Forests." *PLoS One* 10, no. 9: e0139214. <https://doi.org/10.1371/journal.pone.0139214>.

Barrere, J., B. Reineking, T. Cordonnier, et al. 2023. "Functional Traits and Climate Drive Interspecific Differences in Disturbance-Induced Tree Mortality." *Global Change Biology* 29: gcb.16630. <https://doi.org/10.1111/gcb.16630>.

Borghi, C., S. Francini, R. E. McRoberts, et al. 2024. "Country-Wide Assessment of Biodiversity, Naturalness and Old-Growth Status Using National Forest Inventory Data." *European Journal of Forest Research* 143: 271–303. <https://doi.org/10.1007/s10342-023-01620-6>.

Bouchard, M., D. Kneeshaw, and Y. Bergeron. 2006. "Forest Dynamics After Successive Spruce Budworm Outbreaks in Mixedwood Forests." *Ecology* 87, no. 9: 2319–2329. [https://doi.org/10.1890/0012-9658\(2006\)87\[2319:FDASSB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2319:FDASSB]2.0.CO;2).

Braziunas, K. H., W. D. Hansen, R. Seidl, W. Rammer, and M. G. Turner. 2018. "Looking Beyond the Mean: Drivers of Variability in Postfire Stand Development of Conifers in Greater Yellowstone." *Forest Ecology and Management* 430: 460–471. <https://doi.org/10.1016/j.foreco.2018.08.034>.

Buma, B. 2015. "Disturbance Interactions: Characterization, Prediction, and the Potential for Cascading Effects." *Ecosphere* 6, no. 4: 1–15. <https://doi.org/10.1890/ES15-00058.1>.

Buma, B., S. Weiss, K. Hayes, and M. Lucash. 2020. "Wildland Fire Reburning Trends Across the US West Suggest Only Short-Term Negative Feedback and Differing Climatic Effects." *Environmental Research Letters* 15, no. 3: 034026. <https://doi.org/10.1088/1748-9326/ab6c70>.

Cannon, J. B., S. K. Henderson, M. H. Bailey, and C. J. Peterson. 2019. "Interactions Between Wind and Fire Disturbance in Forests: Competing Amplifying and Buffering Effects." *Forest Ecology and Management* 436: 117–128. <https://doi.org/10.1016/j.foreco.2019.01.015>.

Cannon, J. B., C. J. Peterson, J. J. O'Brien, and J. S. Brewer. 2017. "A Review and Classification of Interactions Between Forest Disturbance From Wind and Fire." *Forest Ecology and Management* 406: 381–390. <https://doi.org/10.1016/j.foreco.2017.07.035>.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. "Towards a Worldwide Wood Economics Spectrum." *Ecology Letters* 12, no. 4: 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.

Choi, D. H., E. A. LaRue, J. W. Atkins, et al. 2023. "Short-Term Effects of Moderate Severity Disturbances on Forest Canopy Structure." *Journal of Ecology* 111, no. 9: 1866–1881. <https://doi.org/10.1111/1365-2745.14145>.

Connell, J. H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs: High Diversity of Trees and Corals Is Maintained Only in a

- Nonequilibrium State." *Science* 199, no. 4335: 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>.
- Copernicus Climate Change Service, and Climate Data Store. 2019. "Fire Danger Indices Historical Data From the Copernicus Emergency Management Service." Copernicus Climate Change Service (C3S) Climate Data Store (CDS). <https://doi.org/10.24381/cds.0e89c522>.
- Dorfman, R. 1979. *Economic Theory and Public Decisions*, 512. Edward Elgar Publishing. <https://doi.org/10.4337/9781035334919>.
- Dunn, P. K., and G. K. Smyth. 2018. *Generalized Linear Models With Examples in R*. 1st ed. Springer. <https://doi.org/10.1007/978-1-4419-0118-7>.
- Dupuy, J., H. Fargeon, N. Martin-StPaul, et al. 2020. "Climate Change Impact on Future Wildfire Danger and Activity in Southern Europe: A Review." *Annals of Forest Science* 77, no. 2: 35. <https://doi.org/10.1007/s13595-020-00933-5>.
- Everham, E. M., and N. V. L. Brokaw. 1996. "Forest Damage and Recovery From Catastrophic Wind." *Botanical Review* 62, no. 2: 113–185. <https://doi.org/10.1007/BF02857920>.
- Fahey, R. T., J. W. Atkins, J. L. Campbell, et al. 2020. "Effects of an Experimental Ice Storm on Forest Canopy Structure." *Canadian Journal of Forest Research* 50, no. 2: 136–145. <https://doi.org/10.1139/cjfr-2019-0276>.
- Felton, A., S. Belyazid, J. Eggers, E.-M. Nordström, and K. Öhman. 2024. "Climate Change Adaptation and Mitigation Strategies for Production Forests: Trade-Offs, Synergies, and Uncertainties in Biodiversity and Ecosystem Services Delivery in Northern Europe." *Ambio* 53, no. 1: 1–16. <https://doi.org/10.1007/s13280-023-01909-1>.
- Foster, D. R. 1988. "Species and Stand Response to Catastrophic Wind in Central New England, U.S.A." *Journal of Ecology* 76, no. 1: 135. <https://doi.org/10.2307/2260458>.
- Gao, T., M. Hedblom, T. Emilsson, and A. B. Nielsen. 2014. "The Role of Forest Stand Structure as Biodiversity Indicator." *Forest Ecology and Management* 330: 82–93. <https://doi.org/10.1016/j.foreco.2014.07.007>.
- Gardiner, B., K. Blennow, J.-M. Carnus, et al. 2010. "Destructive Storms in European Forests: Past and Forthcoming Impacts." <https://hal.inrae.fr/hal-02824530>.
- Gauthier, S., D. Boucher, J. Morissette, and L. De Grandpré. 2010. "Fifty-Seven Years of Composition Change in the Eastern Boreal Forest of Canada." *Journal of Vegetation Science* 21, no. 4: 772–785. <https://doi.org/10.1111/j.1654-1103.2010.01186.x>.
- Georgi, L., M. Kunz, A. Fichtner, A. Bienert, H.-G. Maas, and G. Von Oheimb. 2022. "Effects of Tree Diversity on Canopy Space Occupation Vary With Tree Size and Canopy Space Definition in a Mature Broad-Leaved Forest." *Agricultural and Forest Meteorology* 323: 109055. <https://doi.org/10.1016/j.agrformet.2022.109055>.
- González, J. R., A. Trasobares, M. Palahí, and T. Pukkala. 2007. "Predicting Stand Damage and Tree Survival in Burned Forests in Catalonia (North-East Spain)." *Annales of Forest Science* 64: 733–742. <https://doi.org/10.1051/forest:2007053>.
- Gough, C. M., J. W. Atkins, R. T. Fahey, et al. 2022. "Disturbance Has Variable Effects on the Structural Complexity of a Temperate Forest Landscape." *Ecological Indicators* 140: 109004. <https://doi.org/10.1016/j.ecolind.2022.109004>.
- Greenwood, S., P. Ruiz-Benito, J. Martínez-Vilalta, et al. 2017. "Tree Mortality Across Biomes Is Promoted by Drought Intensity, Lower Wood Density and Higher Specific Leaf Area." *Ecology Letters* 20, no. 4: 539–553. <https://doi.org/10.1111/ele.12748>.
- Grimm, V., and C. Wissel. 1997. "Babel, or the Ecological Stability Discussions: An Inventory and Analysis of Terminology and a Guide for Avoiding Confusion." *Oecologia* 109, no. 3: 323–334. <https://doi.org/10.1007/s004420050090>.
- Guyot, V., B. Castagneyrol, A. Vialatte, M. Deconchat, and H. Jactel. 2016. "Tree Diversity Reduces Pest Damage in Mature Forests Across Europe." *Biology Letters* 12: 20151037. <https://doi.org/10.1098/rsbl.2015.1037>.
- Haber, L. T., R. T. Fahey, S. B. Wales, et al. 2020. "Forest Structure, Diversity, and Primary Production in Relation to Disturbance Severity." *Ecology and Evolution* 10, no. 10: 4419–4430. <https://doi.org/10.1002/ece3.6209>.
- Halpern, C. B. 1988. "Early successional pathways and the resistance and resilience of forest communities." *Ecology* 69, no. 6: 1703–1715. <https://doi.org/10.2307/1941148>.
- Halpin, C. R., and C. G. Lorimer. 2016. "Trajectories and Resilience of Stand Structure in Response to Variable Disturbance Severities in Northern Hardwoods." *Forest Ecology and Management* 365: 69–82. <https://doi.org/10.1016/j.foreco.2016.01.016>.
- Hanewinkel, M., T. Kuhn, H. Bugmann, A. Lanz, and P. Brang. 2014. "Vulnerability of Uneven-Aged Forests to Storm Damage." *Forestry* 87, no. 4: 525–534. <https://doi.org/10.1093/forestry/cpu008>.
- Hart, S. J., T. T. Veblen, N. Mietkiewicz, and D. Kulakowski. 2015. "Negative Feedbacks on Bark Beetle Outbreaks: Widespread and Severe Spruce Beetle Infestation Restricts Subsequent Infestation." *PLoS One* 10: e0127975.
- Hekkala, A.-M., M. Jönsson, S. Kärvmö, J. Strengbom, and J. Sjögren. 2023. "Habitat Heterogeneity Is a Good Predictor of Boreal Forest Biodiversity." *Ecological Indicators* 148: 110069. <https://doi.org/10.1016/j.ecolind.2023.110069>.
- Hill, M. O. 1973. "Diversity and Evenness: A Unifying Notation and Its Consequences." *Ecology* 54, no. 2: 427–432. <https://doi.org/10.2307/1934352>.
- Hlásny, T., S. Zimová, K. Merganičová, P. Štěpánek, R. Modlinger, and M. Turčáni. 2021. "Devastating Outbreak of Bark Beetles in The Czech Republic: Drivers, Impacts, and Management Implications." *Forest Ecology and Management* 490: 119075. <https://doi.org/10.1016/j.foreco.2021.119075>.
- Huston, M. A. 1997. "Hidden Treatments in Ecological Experiments: Re-Evaluating the Ecosystem Function of Biodiversity." *Oecologia* 110, no. 4: 449–460. <https://doi.org/10.1007/s004420050180>.
- Isbell, F., D. Craven, J. Connolly, et al. 2015. "Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes." *Nature* 526, no. 7574: 574–577. <https://doi.org/10.1038/nature15374>.
- Jactel, H., J. Bauhus, J. Boberg, et al. 2017. "Tree Diversity Drives Forest Stand Resistance to Natural Disturbances." *Current Forestry Reports* 3, no. 3: 223–243. <https://doi.org/10.1007/s40725-017-0064-1>.
- Jactel, H., and E. G. Brockerhoff. 2007. "Tree Diversity Reduces Herbivory by Forest Insects." *Ecology Letters* 10: 835–848. <https://doi.org/10.1111/j.1461-0248.2007.01073.x>.
- Jactel, H., X. Moreira, and B. Castagneyrol. 2021. "Tree Diversity and Forest Resistance to Insect Pests: Patterns, Mechanisms, and Prospects." *Annual Review of Entomology* 66: 277–296.
- Jost, L. 2006. "Entropy and Diversity." *Oikos* 113, no. 2: 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>.
- Kafka, V., S. Gauthier, and Y. Bergeron. 2001. "Fire Impacts and Crowning in the Boreal Forest: Study of a Large Wildfire in Western Quebec." *International Journal of Wildland Fire* 10, no. 2: 119. <https://doi.org/10.1071/WF01012>.
- Kattge, J., S. Díaz, S. Lavorel, et al. 2011. "TRY—A Global Database of Plant Traits: Try—A Global Database of Plant Traits." *Global Change Biology* 17, no. 9: 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>.
- Keeley, J. E. 2009. "Fire Intensity, Fire Severity and Burn Severity: A Brief Review and Suggested Usage." *International Journal of Wildland Fire* 18, no. 1: 116–126. <https://doi.org/10.1071/WF07049>.

- Kosmidis, I., and A. Zeileis. 2025. "Extended-Support Beta Regression for [0, 1] Responses. *Journal of the Royal Statistical Society Series C.*" *Applied Statistics*: qlaf039. <https://doi.org/10.1093/jrsssc/qlaf039>.
- Kulha, N., A. Ahokas, S. Gauthier, and T. Aakala. 2023. "Race to the Canopy: The Development of Tree Size Hierarchies Following a Partial Disturbance in a Boreal Old-Growth Forest." *Canadian Journal of Forest Research* 53: 996–1005. <https://doi.org/10.1139/cjfr-2022-0224>.
- Kulha, N., J. Heikkinen, J. Holder, et al. 2024. "Landscape Configuration and Storm Characteristics Drive Spatial Patterns of Wind Disturbance in Boreal Forest Landscapes." *Landscape Ecology* 39: 119.
- Kulha, N., J. Honkaniemi, J. Barrere, et al. 2023. "Competition-Induced Tree Mortality Across Europe Is Driven by Shade Tolerance, Proportion of Conspecifics and Drought." *Journal of Ecology* 111, no. 10: 2310–2323. <https://doi.org/10.1111/1365-2745.14184>.
- Kunstler, G., A. Guyennon, S. Ratcliffe, et al. 2021. "Demographic Performance of European Tree Species at Their Hot and Cold Climatic Edges." *Journal of Ecology* 109, no. 2: 1041–1054. <https://doi.org/10.1111/1365-2745.13533>.
- Laapas, M., S. Suvanto, M. Peltoniemi, and A. Venäläinen. 2023. "Combining Interpolated Maximum Wind Gust Speed and Forest Vulnerability for Rapid Post-Storm Mapping of Potential Forest Damage Areas in Finland." *Forestry* 96, no. 5: 690–704. <https://doi.org/10.1093/forestry/cpad005>.
- Lännenpää, A., T. Aakala, H. Kauhanen, and T. Kuuluvainen. 2008. "Tree Mortality Agents in Pristine Norway Spruce Forests in Northern Fennoscandia." *Silva Fennica* 42, no. 2: 151–163.
- Lecina-Diaz, J., C. Senf, M. Grünig, and R. Seidl. 2024. "Ecosystem Services at Risk From Disturbance in Europe's Forests." *Global Change Biology* 30, no. 3: e17242. <https://doi.org/10.1111/gcb.17242>.
- Leverkus, A. B., D. B. Lindenmayer, S. Thorn, and L. Gustafsson. 2018. "Salvage Logging in the World's Forests: Interactions Between Natural Disturbance and Logging Need Recognition." *Global Ecology and Biogeography* 27, no. 10: 1140–1154. <https://doi.org/10.1111/gcb.12772>.
- Messier, C., J. Bauhus, R. Sousa-Silva, et al. 2022. "For the Sake of Resilience and Multifunctionality, Let's Diversify Planted Forests!" *Conservation Letters* 15, no. 1: e12829. <https://doi.org/10.1111/conl.12829>.
- Michaletz, S. T., and E. A. Johnson. 2007. "How Forest Fires Kill Trees: A Review of the Fundamental Biophysical Processes." *Scandinavian Journal of Forest Research* 22, no. 6: 500–515. <https://doi.org/10.1080/02827580701803544>.
- Miquelajauregui, Y., S. G. Cumming, and S. Gauthier. 2016. "Modelling Variable Fire Severity in Boreal Forests: Effects of Fire Intensity and Stand Structure." *PLoS One* 11, no. 2: e0150073. <https://doi.org/10.1371/journal.pone.0150073>.
- Mitchell, J. C., D. M. Kashian, X. Chen, et al. 2023. "Forest Ecosystem Properties Emerge From Interactions of Structure and Disturbance." *Frontiers in Ecology and the Environment* 21, no. 1: 14–23. <https://doi.org/10.1002/fee.2589>.
- Mitchell, S. J. 2013. "Wind as a Natural Disturbance Agent in Forests: A Synthesis." *Forestry* 86, no. 2: 147–157. <https://doi.org/10.1093/forestry/cps058>.
- Morimoto, J., K. Nakagawa, K. T. Takano, et al. 2019. "Comparison of Vulnerability to Catastrophic Wind Between Abies Plantation Forests and Natural Mixed Forests in Northern Japan." *Forestry: An International Journal of Forest Research* 92, no. 4: 436–443. <https://doi.org/10.1093/forestry/cpy045>.
- Muñoz Sabater, J. 2019. "ERA5-Land Monthly Averaged Data From 1950 to Present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS)." <https://doi.org/10.24381/cds.68d2bb30>.
- Nagel, T. A., D. Firm, and A. Rozman. 2021. "Intermediate Disturbances Are a Key Driver of Long-Term Tree Demography Across Old-Growth Temperate Forests." *Ecology and Evolution* 11: ece3.8320. <https://doi.org/10.1002/ece3.8320>.
- Niklasson, M., and A. Granström. 2000. "Numbers and Sizes of Fires: Long-Term Spatially Explicit Fire History in a Swedish Boreal Landscape." *Ecology* 81, no. 6: 1484–1499. [https://doi.org/10.1890/0012-9658\(2000\)081\[1484:NASOFL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1484:NASOFL]2.0.CO;2).
- Nykänen, M.-L., M. Broadgate, S. Kellomäki, H. Peltola, and C. Quine. 1997. "Factors Affecting Snow Damage of Trees With Particular Reference to European Conditions." *Silva Fennica* 31, no. 2: 193–213. <https://doi.org/10.14214/sf.a8519>.
- Patacca, M., M. Lindner, M. E. Lucas-Borja, et al. 2022. "Significant Increase in Natural Disturbance Impacts on European Forests Since 1950." *Global Change Biology* 29, no. 5: 1359–1376. <https://doi.org/10.1111/gcb.16531>.
- Peris-Llopis, M., B. Mola-Yudego, F. Berninger, J. Garcia-Gonzalo, and J. R. González-Olabarria. 2024. "Impact of Species Composition on Fire-Induced Stand Damage in Spanish Forests." *Scientific Reports* 14, no. 1: 8594. <https://doi.org/10.1038/s41598-024-59210-4>.
- Peterson, C. 2019. "Damage Diversity as a Metric of Structural Complexity After Forest Wind Disturbance." *Forests* 10, no. 2: 85. <https://doi.org/10.3390/f10020085>.
- Pimm, S. L. 1984. "The Complexity and Stability of Ecosystems." *Nature* 307, no. 5949: 321–326. <https://doi.org/10.1038/307321a0>.
- Pukkala, T., O. Laiho, and E. Lähde. 2016. "Continuous Cover Management Reduces Wind Damage." *Forest Ecology and Management* 372: 120–127. <https://doi.org/10.1016/j.foreco.2016.04.014>.
- R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Reyes, G. P., D. Kneeshaw, L. De Grandpré, and A. Leduc. 2010. "Changes in Woody Vegetation Abundance and Diversity After Natural Disturbances Causing Different Levels of Mortality." *Journal of Vegetation Science* 21, no. 2: 406–417. <https://doi.org/10.1111/j.1654-1103.2009.01152.x>.
- Schmitt, A., R. Trouvé, I. Seynave, and F. Lebourgeois. 2020. "Decreasing Stand Density Favors Resistance, Resilience, and Recovery of *Quercus petraea* Trees to a Severe Drought, Particularly on Dry Sites." *Annals of Forest Science* 77, no. 2: 52. <https://doi.org/10.1007/s13595-020-00959-9>.
- Seidl, R., J. Honkaniemi, T. Aakala, et al. 2020. "Globally Consistent Climate Sensitivity of Natural Disturbances Across Boreal and Temperate Forest Ecosystems." *Ecography* 43, no. 7: 967–978. <https://doi.org/10.1111/ecog.04995>.
- Seidl, R., D. Thom, M. Kautz, et al. 2017. "Forest Disturbances Under Climate Change." *Nature Climate Change* 7, no. 6: 395–402. <https://doi.org/10.1038/nclimate3303>.
- Seidl, R., and M. G. Turner. 2022. "Post-Disturbance Reorganization of Forest Ecosystems in a Changing World." *Proceedings of the National Academy of Sciences of the United States of America* 119, no. 28: e2202190119. <https://doi.org/10.1073/pnas.2202190119>.
- Senf, C., D. Pflugmacher, Y. Zhiqiang, et al. 2018. "Canopy Mortality Has Doubled in Europe's Temperate Forests Over the Last Three Decades." *Nature Communications* 9, no. 1: 4978. <https://doi.org/10.1038/s41467-018-07539-6>.
- Senf, C., and R. Seidl. 2021a. "Mapping the Forest Disturbance Regimes of Europe." *Nature Sustainability* 4, no. 1: 63–70. <https://doi.org/10.1038/s41893-020-00609-y>.
- Senf, C., and R. Seidl. 2021b. "Storm and Fire Disturbances in Europe: Distribution and Trends." *Global Change Biology* 27: gcb.15679. <https://doi.org/10.1111/gcb.15679>.

- Siipilehto, J., M. Allen, U. Nilsson, et al. 2020. "Stand-Level Mortality Models for Nordic Boreal Forests." *Silva Fennica* 54, no. 5: 10414. <https://doi.org/10.14214/sf.10414>.
- Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2011. "Do Mountain Pine Beetle Outbreaks Change the Probability of Active Crown Fire in Lodgepole Pine Forests?" *Ecological Monographs* 81, no. 1: 3–24. <https://doi.org/10.1890/10-1176.1>.
- Sommerfeld, A., W. Rammer, M. Heurich, T. Hilmers, J. Müller, and R. Seidl. 2021. "Do Bark Beetle Outbreaks Amplify or Dampen Future Bark Beetle Disturbances in Central Europe?" *Journal of Ecology* 109, no. 2: 737–749. <https://doi.org/10.1111/1365-2745.13502>.
- Spellerberg, I. F., and P. J. Fedor. 2003. "A Tribute to Claude Shannon (1916–2001) and a Plea for More Rigorous Use of Species Richness, Species Diversity and the 'Shannon-Wiener' Index." *Global Ecology and Biogeography* 12: 177–179. <https://doi.org/10.1046/j.1466-822X.2003.00015.x>.
- Stevens, J. T., M. M. Kling, D. W. Schwilk, J. M. Varner, and J. M. Kane. 2020. "Biogeography of Fire Regimes in Western U.S. Conifer Forests: A Trait-Based Approach." *Global Ecology and Biogeography* 29, no. 5: 944–955. <https://doi.org/10.1111/geb.13079>.
- Stovall, A. E. L., H. Shugart, and X. Yang. 2019. "Tree Height Explains Mortality Risk During an Intense Drought." *Nature Communications* 10, no. 1: 4385. <https://doi.org/10.1038/s41467-019-12380-6>.
- Stuart-Haëntjens, E. J., P. S. Curtis, R. T. Fahey, C. S. Vogel, and C. M. Gough. 2015. "Net Primary Production of a Temperate Deciduous Forest Exhibits a Threshold Response to Increasing Disturbance Severity." *Ecology* 96, no. 9: 2478–2487. <https://doi.org/10.1890/14-1810.1>.
- Suvanto, S., A. Esquivel-Muelbert, M.-J. Schelhaas, et al. 2025. "Understanding Europe's Forest Harvesting Regimes." *Earth's Future* 13, no. 2: e2024EF005225. <https://doi.org/10.1029/2024EF005225>.
- Suvanto, S., A. Lehtonen, S. Nevalainen, et al. 2020. "Mapping the Probability of Forest Snow Disturbances in Finland." *PLoS One* 16, no. 7: e0254876. <https://doi.org/10.1101/2020.12.23.424139>.
- Takala, M., K. Luojus, J. Pulliainen, et al. 2011. "Estimating Northern Hemisphere Snow Water Equivalent for Climate Research Through Assimilation of Space-Borne Radiometer Data and Ground-Based Measurements." *Remote Sensing of Environment* 115, no. 12: 3517–3529. <https://doi.org/10.1016/j.rse.2011.08.014>.
- Tilman, D. 1997. "Community Invasibility, Recruitment Limitation, and Grassland Biodiversity." *Ecology* 78, no. 1: 81–92. [https://doi.org/10.1890/0012-9658\(1997\)078\[0081:CIRLAG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2).
- Tilman, D. 2001. "Functional Diversity." In *Encyclopedia of Biodiversity*, edited by S. A. Levin. Academic Press.
- Trouvé, R., L. Osborne, and P. J. Baker. 2021. "The Effect of Species, Size, and Fire Intensity on Tree Mortality Within a Catastrophic Bushfire Complex." *Ecological Applications* 31, no. 6: e02383. <https://doi.org/10.1002/eap.2383>.
- Turner, M. G., and R. Seidl. 2023. "Novel Disturbance Regimes and Ecological Responses." *Annual Review of Ecology, Evolution, and Systematics* 54: 63–83. <https://doi.org/10.1146/annurev-ecolsys-110421-101120>.
- Valbuena, R. 2015. "Forest Structure Indicators Based on Tree Size Inequality and Their Relationships to Airborne Laser Scanning." *Dissertationes Forestales* 2015, no. 205: 87. <https://doi.org/10.14214/df.205>.
- Valbuena, R., P. Packalén, S. Marti'n-Fernández, and M. Maltamo. 2012. "Diversity and Equitability Ordering Profiles Applied to Study Forest Structure." *Forest Ecology and Management* 276: 185–195. <https://doi.org/10.1016/j.foreco.2012.03.036>.
- Valta, H., I. Lehtonen, T. K. Laurila, A. Venäläinen, M. Laapas, and H. Gregow. 2019. "Communicating the Amount of Windstorm Induced Forest Damage by the Maximum Wind Gust Speed in Finland." *Advances in Science and Research* 16: 31–37. <https://doi.org/10.5194/asr-16-31-2019>.
- Viljur, M., S. R. Abella, M. Adámek, et al. 2022. "The Effect of Natural Disturbances on Forest Biodiversity: An Ecological Synthesis." *Biological Reviews* 97, no. 5: 1930–1947. <https://doi.org/10.1111/brv.12876>.
- Vitolo, C., F. Di Giuseppe, C. Barnard, et al. 2020. "ERA5-Based Global Meteorological Wildfire Danger Maps." *Scientific Data* 7, no. 1: 216. <https://doi.org/10.1038/s41597-020-0554-z>.
- Weeks, B. C., S. P. Hamburg, and M. A. Vadeboncoeur. 2009. "Ice Storm Effects on the Canopy Structure of a Northern Hardwood Forest After 8 Years." *Canadian Journal of Forest Research* 39, no. 8: 1475–1483. <https://doi.org/10.1139/X09-076>.
- Woods, K. D. 2004. "Intermediate Disturbance in a Late-Successional Hemlock-Northern Hardwood Forest." *Journal of Ecology* 92, no. 3: 464–476. <https://www.jstor.org/stable/3599504>.
- Yachi, S., and M. Loreau. 1999. "Biodiversity and Ecosystem Productivity in a Fluctuating Environment: The Insurance Hypothesis." *Proceedings of the National Academy of Sciences* 96, no. 4: 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>.

### Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70106-sup-0001-Supinfo.docx.