Functional traits and climate drive interspecific differences in disturbance-induced tree mortality

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1   Abstract

With climate change, natural disturbances such as storm or fire are reshuffled, inducing pervasive shifts in forest dynamics. To predict how it will impact forest structure and composition, it is crucial to understand how tree species differ in their sensitivity to disturbances. In this study, we investigated how functional traits and species mean climate affect their sensitivity to disturbances while controlling for tree size and stand structure.

With data on 130594 trees located on 7617 plots that were disturbed by storm, fire, snow, biotic or other disturbances from the French, Spanish and Finnish National Forest Inventory, we modeled annual mortality probability for 40 European tree species as a function of tree size, dominance status, disturbance type and intensity. We tested the correlation of our estimated species probability of disturbance-mortality with their traits and their mean climate niches.

We found that different trait combinations controlled species sensitivity to disturbances. Storm-sensitive species had a high height-dbh ratio, low wood density and high maximum growth, while fire-sensitive species had low bark thickness and high P50. Species from warmer and drier climates, where fires are more frequent, were more resistant to fire. The ranking in disturbance sensitivity between species was overall consistent across disturbance types. Productive conifer species were the most disturbance-sensitive, while Mediterranean oaks were the least disturbance-sensitive.

Our study identified key relations between species functional traits and disturbance sensitivity, that allows more reliable predictions of how changing climate and disturbance regimes will impact future forest structure and species composition at large spatial scales.

Key-words: tree mortality, environmental change, disturbance vulnerability, trait ecology, Bayesian inference, National Forest Inventory

2 Introduction

Over the last decades, tree mortality events have been reported to increase across the globe (Allen et al., 2010; Senf et al., 2018; Taccoen et al., 2019; Yi et al., 2022), thereby threatening the numerous ecosystem services provided by forests (Thom and Seidl, 2016). Increasing tree mortality can partly be attributed to climate change via the influence of climate on the two major processes driving tree death: background mortality and disturbance mortality (Franklin et al., 1987). First, changing climatic conditions have been associated with increasing rates of background mortality - *i.e.,* low severity mortality events occurring steadily in time and space in the absence of catastrophic events - both in Europe (Neumann et al., 2017; Taccoen et al., 2019; Changenet et al., 2021) and in North America (Hember et al., 2017). Increasing climate-induced background mortality is mainly attributed to water-stress through increased temperature and/or decreased precipitation (Bauman et al., 2022), but also to increased stand densities that partly derive from climate change (Kulha et al., 2020). Second, several studies have shown that climate change is also the main factor contributing to the current increase in the magnitude, frequency and size of natural disturbances (Schelhaas et al., 2003; Seidl et al., 2017, 2020; Senf and Seidl, 2021a). Climate contribution to changing disturbance regimes varies across disturbance agents (Seidl et al., 2017). For instance, fire is most often attributed to hotter and drier conditions (Halofsky et al., 2020; Xu et al., 2020), biotic disturbances are notably promoted by milder winters (Weed et al., 2013) while for windthrow, the effect of climate might mainly result in a shift in storm tracks (Seneviratne et al., 2021). Disturbances have a particularly strong effect on forest dynamics through their impact on tree mortality, reducing forest age and shifting species composition at global scale (McDowell et al., 2020). Understanding the drivers of disturbance-induced mortality is therefore critical to forecast how forests respond to climate change.

The intensity of disturbance exposure - *e.g.,* wind speed, fire energy - is the primary factor determining disturbance-induced mortality (Canham et al., 2001; Trouvé et al., 2021). However, all trees are not equally impacted by a disturbance within a stand. At the tree level, studies agree that tree size, and more particularly tree height, is one of the main factors affecting tree sensitivity to disturbances such as wind (Canham et al., 2001; Gardiner et al., 2010; Suvanto et al., 2019), fire (Brando et al., 2012; Trouvé et al., 2021) or snow (Nykänen et al., 1997), but with an effect that depends on the disturbance agent. Tree height have been shown to increase susceptibility to both storm (Canham et al., 2001; Díaz-Yáñez et al., 2019; Gardiner, 2021) and snow (Nykänen et al., 1997). For storm mortality, this derives from the fact that the lever arm exerted by wind on the crown of taller trees is higher (Gardiner, 2021). An indirect effect of size is also the social status of the tree within the stand: trees above the average canopy height (hereafter dominant trees) can be more impacted by wind or snow as they are simply more exposed than the dominated trees (Gardiner et al.,

2010). In contrast, smaller or thinner trees are in theory more sensitive to fire due to their thinner bark (Michaletz and Johnson, 2007), which is confirmed by several empirical studies that found a strong negative effect of tree size on fire mortality (Brando et al., 2012; Trouvé et al., 2021). Contrary to abiotic agents, the effect of tree size on sensitivity to biotic disturbances is more complex as it strongly depends on the biotic agent (Das et al., 2016; Fettig et al., 2019; Koontz et al., 2021).

Beyond tree size, inter-specific variations in disturbance sensitivity have also been observed (Canham et al., 2001; Díaz-Yáñez et al., 2019; Trouvé et al., 2021), partially attributed to species-level differences in functional traits. Local studies focused on a few species have shown that species with a thick bark and/or denser wood tend to be more resistant to fire (Brando et al., 2012; Catry et al., 2012; Frejaville et al., 2013), and that species with low height to diameter ratio are less susceptible to storms (Gardiner, 2021). But whether these traits effects hold true for all the dominant species of a continent, and extend to a broader spectrum of functional traits remain to be determined. In addition to functional traits, inter-specific variation in disturbance sensitivity could also result from differences in the climate and disturbance regimes experienced by species throughout their evolutionary history. Indeed, recurrent disturbances can exert a strong evolutionary pressure on tree species to select for disturbance adaptive traits (Johnstone et al., 2016). For instance, fire have been documented to select traits facilitating post-disturbance regeneration such as resprouting or serotiny (Keeley et al., 2011; Keeley and Pausas, 2022). Similarly, we could expect tree species to be more resistant to a specific disturbance if they have evolved in areas where this disturbance is frequent. However, whether disturbance regimes have selected species traits promoting resistance strategies following different disturbance types is still unknown.

Studies that have investigated the drivers of disturbance-induced mortality so far are mostly local and/or focused on a certain type of disturbance. This is mainly due to the difficulty to find disturbance datasets with a sufficiently broad temporal and/or spatial extent. Significant progress is being made on that issue with the analysis of satellite data (Senf and Seidl, 2021a,b), but these data are generally too coarse to identify differences in disturbance-induced mortality between species or individuals. Local studies can bring crucial information on how certain tree-level or stand-level characteristics influence tree susceptibility to a specific disturbance, but their small spatial extent generally makes the comparison of several disturbance types particularly difficult. It remains thus unknown whether the effects of tree-level characteristics (e.g., size, dominance) and species traits observed in local studies hold true at continental scale. Furthermore, as forests are exposed to changing disturbance regimes, identifying functional traits predicting consistently species sensitivity to each disturbance type would help forecast species response to new disturbance regimes and contribute to improve forest adaptation to climate change. Over the last decades, an

increasing number of European national forest inventories (NFI) started to monitor disturbance impacts at the tree or stand level, thereby providing a unique opportunity to investigate the drivers of disturbance-induced tree mortality at broad spatial scale, both at the tree-level and species level.

Using NFI data from three countries covering the main climate and disturbance types in Europe (Spain, France and Finland) from 1997 to 2020, we investigated how tree sensitivity to storm, fire, biotic and snow disturbances is influenced by (i) tree size and dominance, (ii) species functional traits, and by (iii) the mean climate in species distribution area.

3   Material and methods

3.1   Data presentation

3.1.1   National Forest Inventory data

We used National Forest Inventories data of three European countries (France, Spain and Finland) that reported if a plot or a tree experienced a disturbance between two inventories. Since our analytical approach requires knowing whether a disturbance event occurred in a stand between two inventories, we restricted our analysis to countries that reported this information. In France, only three disturbance categories are reported - i.e., windstorm, fire and "other", the latter category including any other disturbance type - whereas in Spain and Finland, the classification includes biotic and snow disturbance in addition to storm and fire. The Spanish, French and Finnish NFI respectively report disturbances at tree-level, NFI plot-level and stand-level (in Finland, stand designates an area larger than the NFI plot sampled). In the three countries, we used the same criteria to define a disturbed plot - *i.e.,* affected by a disturbance (information derived from tree-level in Spain) that caused the death of at least one tree within the plot between the two censuses. As our analysis focuses on disturbance-related mortality, we only used the NFI plots that were classified as disturbed. The number of plots and trees included per country and per disturbance type is reported in supporting information A, table S1.

In each country, we only considered plots that were measured twice to quantify true mortality events. The time interval between two censuses was systematically 5 years in France, and on average 5 and 10 years in Finland and in Spain, respectively (the time interval is not constant for these two countries). The time period and sampling dates covered by each of these three data sets is reported in supporting information A. The plots are circular, with a different sampling radius depending on tree size (see the detailed protocols for each country in supporting information A).

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Tree-level data includes information on tree diameter at breast height (dbh), species, and status (alive, dead or harvested). Height was also measured but only for a subset of trees within each plot, we thus chose to use dbh instead of height as a proxy for tree size in the analyses. Most NFI-based studies that focused on background mortality excluded plots where harvesting occurred since it is not known whether trees were alive or dead before harvest (see Kunstler et al., 2020, for instance). However, as salvage logging is extremely common in disturbed plots, such criteria would exclude many disturbance events, and could bias the dataset towards stands of low economic value (and thus for which salvage logging is less common) and/or towards stands mostly affected by low-intensity disturbances. Though this can lead to a slight over-estimation of mortality, we chose to keep disturbed plots where harvesting occurred, and to make the assumption that all logging in disturbed plots is salvage logging. This selection led to a total of respectively 5185, 1819, and 613 disturbed plots in Spain, France and Finland, with a relatively constant mortality rate in these disturbed plots across countries (supporting information A, table S1). We excluded trees with a dbh lower than 100 mm at the first census to ensure consistency between the three countries, and we did not consider ingrowth (trees that were measured during the second but not the first census).

3.1.2   Traits data

To investigate how functional traits explain inter-specific differences in disturbance sensitivity, we compiled disturbance-related traits at the species level from various databases - *i.e.,* wood density database (Chave et al., 2009; Zanne et al., 2009), Global Root Traits database (Groot) (Guerrero-Ramírez et al., 2021), shade toler-ance database (Niinemets and Valladares, 2006), P50 databases (Martin-StPaul et al. (2017) and López et al. (2013) for *Pinus canariensis*) and TRY database (Kattge et al., 2020, and see references in supporting information B). We also calculated species-level traits directly from NFI data (*e.g.,* height-to-dbh ratio, bark thickness, maximum growth, see supporting information C for details on the calculation). Traits were selected based on two criteria: relevance regarding the sensitivity to the different disturbances studied, and availability for a sufficient number of species in our dataset. All the traits included in the analysis, their source and the associated hypotheses re-garding disturbance sensitivity are listed in table 1.

3.1.3   Climatic data

To get the mean climatic niche of each species (hereafter species mean climate), we extracted each species occurrence data from the GBIF database (Flemons et al., 2007; GBIF.org, 2022) to have their distribution at global scale (see supporting informa-tion E for details). For each spatial occurrence of each species, we extracted climatic data (*i.e.,* mean annual temperature (mat), precipitation (map), and minimal annual

temperature (tmin) from 1979 to 2013 at 1km x 1km resolution) from the CHELSA portal (Karger et al., 2017, 2018). From this, we calculated species mean climate as the mean of each of these three variables per species across their distribution.

Similarly, to test if species distributed in areas where a disturbance is frequent are more tolerant to this disturbance, we extracted for each species occurrence obtained from GBIF three disturbance-related climatic indices:

- The Fire Weather Index (FWI) (Vitolo et al., 2020) provides a historical reconstruction of meteorological conditions favourable to the start, spread and sustainability of fires at a daily timescale and 28km x 28km spatial resolution. We calculated a species-level FWI as the mean FWI from 2012 to 2021 for each species occurrence point. We chose to only include the last 10 years as the index was spatially consistent between years.

- To quantify previous wind disturbances over species distribution, we retrieved the hourly wind gust at 10m height at 0am, 3am, 6am, 9am, 12am, 3pm, 6pm and 9pm during the winter months (December to February) over 10 years (from 1991 to 2011) from ERA5 database (Hersbach et al., 2018). We computed the 95% quantile at each occurrence point, and calculated a species-level max wind speed as the mean 95% quantile value over all occurrence points of a species.

- We used the Snow Water Equivalent (SWE) (*i.e.,* resulting water column should a snowpack melt in place, calculated based on Takala et al. (2011)), extracted from the GlobSnow database (Luojus et al., 2020), as a proxy for long-term mean snow load conditions. We averaged the mean SWE in winter months from 1979 to 2017 at each species occurrence point to get a species-level SWE.

3.2   Data analysis

3.2.1   Statistical model

Our modelling approach builds on Canham et al. (2001) (see also Canham et al., 2010; Trouvé et al., 2021) and aims at jointly estimating plot-level disturbance intensity and tree-level mortality probability. To facilitate the fit, we fixed the overall distribution of the plot-level disturbance intensity for each disturbance type. The model, then, estimates for each plot its disturbance intensity (drawn from the global distribution) based on the proportion of trees that were killed but also on their characteristics (e.g., species, size). The joint estimation of plot-level disturbance intensity and tree-level mortality probability, is key to estimate inter-specific differences in disturbance sensitivity.

Although background mortality may have co-occurred with disturbance mortality, we assumed it was neglibigle and that disturbances were the main cause of mortality since we only included plots affected by a disturbance that caused mortality. In the NFI plots included in this study, we considered that plots could only be disturbed by one unique disturbance type to simplify the analysis. In Spain where disturbances are reported at tree level, we kept the disturbance that affected the highest number of trees in the plot (the proportion of the disturbed plots where at least two disturbances each affected more than one tree was only 0.6%). In Finland, we kept the most important disturbance agent - *i.e.,* at the plot-level, disturbances were ranked based on the reduction in stand quality. In France, only one disturbance was reported per plot. The probability for a tree i in a plot j affected by disturbance k to die (p_{ijk}) was modeled as:

$$p_{ijk} = 1 - (1 - pd_{ijk})^{\Delta t} \tag{1}$$

Where Δt is the time separating the two inventories, and pd_{ijk} is the annual probability for tree i, located in plot j to die from disturbance k. We accounted for the effect of time as disturbances can have lagged effect on mortality so that longer time span between censuses can increase the mortality rates observed. We calculated the annual mortality probability pd_{ijk} as:

$$logit(pd_{ijk}) = a0_{s_i,k,co_j} + a1_{s_i,k} * log(\frac{dbh_i}{dqm_j}) + b_{s_i,k} * I_{jk} * dbh_i^{c_{s_i,k}} \tag{2}$$

Where dbh_i is the diameter at breast height (130 cm) of tree i, dqm_j is the mean quadratic diameter of plot j, $\frac{dbh_i}{dqm_j}$ represents the degree of dominance of tree i in plot j, I_{jk} is a latent variable ranging between 0 and 1 representing the intensity of disturbance k on plot j. $a0_{s_i,k,co_j}$, $a1_{s_i,k}$, $b_{s_i,k}$ and $c_{s_i,k}$ are parameters to estimate for each species s_i and each disturbance k. a_0 corresponds to the intercept, a_1 to the dominance effect, b to the effects of disturbance intensity and dbh, and c to the direction and magnitude of the dbh effect. Note that $a0_{s_i,k,co_j}$ is also country specific to account for differences in protocols.

Because the dominance status is a driver known to have a strong influence on storm mortality (Gardiner et al., 2010) and could in theory affect snow mortality but not specifically the other disturbance types, we have set the value of $a1_{s_i,k}$ to 0 when $k \neq storm|snow$. For snow and storm, we also tested an alternative model where the dominance effect was replaced by a stocking effect (*i.e.,* calculated as the cumulative plot basal area per ha), but we eventually kept the model with dominance since it had a better DIC than the model with stocking (analysis not shown) and including both variables would have over-complexified the model.

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Parameters $a0$, a_1, b and c each followed a normal distribution, with priors centered on 0 and a standard deviation of 100 (except for c that had a prior standard deviation of 1 corresponding to a tighter prior regularization due to its extremely strong effect). The parameter b was restricted to positive values to ensure a positive correlation between the latent variable intensity and mortality risk.

For the latent variable I_k (intensity of disturbance k), to simplify the complexity of the model and allow the estimation of the distribution, we used a beta distribution, with prior parameters that matched the distribution of disturbance k severity (*i.e.,* severity in a plot affected by disturbance k being defined as the proportion of dead trees in this plot). This approach is slightly different from Trouvé et al. (2021) who used a uniform distribution between 0 and 1, and from Canham et al. (2001, 2010) who estimated the disturbance intensity as fixed parameters and not a latent variable.

3.2.2 Model fitting

We fitted the model separately for each disturbance type. For a given disturbance, parameters in eq. 2 were estimated for a species if this disturbance affected at least 15 plots where this species is present, and if the plots affected host at east 150 individuals of that species. Otherwise, individuals of that species were aggregated in "other broadleaf" or "other conifer" (around 10% of the trees included in the model).

To ensure consistency between the three countries when fitting a model with all countries together, we also included the plots affected by biotic and snow disturbances in Finland and in Spain when fitting the model for the "other" category. Then, to explore the specific response to biotic and snow disturbances, we refitted a model with only Spain and Finland for these two disturbances.

The models were fitted with a Bayesian framework using the JAGS software (Plummer, 2003) in the R environment (RCoreTeam, 2019). All variables were scaled before fitting the model to a mean of 0 and a standard deviation of 1. We ran three parallel Markov chains with 5000 iterations, a burn-in of 1000 and a thinning rate of 20. We checked convergence by inspecting the chains and checking that Rhat was smaller than 1.1 (see supporting information F).

3.2.3 Species-specific disturbance sensitivity

We used the estimated parameters of eq. 2 to calculate for each species s_i the sensitivity to each disturbance k (S_{k,s_i}) as the probability to die within 5 years for a tree of species s_i, of 250 mm dbh (mean dbh across the dataset), in a plot j with a quadratic diameter of 250 mm, affected by disturbance k of intensity 0.75.

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$$S_{k,s_i} = 1 - (1 - pd_{ijk})^{\Delta t} \quad \text{with} \quad \begin{cases} dbh_i = dqm_j = 250mm \\ I_{jk} = 0.75 \\ \Delta t = 5 \end{cases} \tag{3}$$

Where pd_{ijk} is the probability described in eq. 2. As the model estimates one set of parameters per mcmc iteration, we kept the mean value of sensitivity across all posterior mcmc iterations. For each mcmc iteration, we averaged the country-specific intercept (a_0 in eq. 2) with a weight equal to the number of observations per country, to account for the uneven number of plots across the three countries. We used a high reference disturbance (*i.e.,* 0.75) intensity to show more clearly species difference in their sensitivity to the disturbance and we used 5 years to account for potential cumulative effect on mortality following disturbance. We verified that the ranking in species sensitivity was overall consistent for different dbh values (100 mm and 400 mm).

3.2.4   Relation between traits and disturbance sensitivity

Effect of traits on the sensitivity to specific disturbances - To study the effect of traits on disturbance sensitivity, we fitted for each trait T_{s_i} presented in table 1 and each disturbance k a linear model with the logit of sensitivity to disturbance k as response variable (S_{k,s_i}) and the centered and scaled trait value as explanatory variable. To account for the uncertainty around the parameters estimated by the bayesian model (eq. 2), we included in each model a weight corresponding to the inverse of the variance of S_{k,s_i} (calculated on logit scale). Because of the potentially large differences in functional traits between broadleaf and conifer, we also fitted the same models but separately for broadleaf and conifer species.

Effect of traits on the sensitivity to all disturbance types together To test whether some traits could confer resistance to multiple disturbances, we also fitted for each trait a linear model with as response variable the logit of sensitivity to each disturbance types (instead of fitting one model per disturbance type), and the centered and scaled trait value as explanatory variable. We also added a random species intercept to account for the multiple observations of sensitivity per species (one species observation per disturbance type). To account for the uncertainty around disturbance sensitivity estimation, we included a weight calculated as the inverse of the variance around disturbance sensitivity.

3.2.5   Relation between species mean climate and disturbance sensitivity

Effect of species mean climate - To test the effect of species mean climate on sensitivity, we first conducted a principal component analysis (PCA) with the three climatic

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variables extracted - i.e., mean annual temperature (mat), minimum annual temperature (tmin) and annual precipitation (map). Then, we fitted for each disturbance type k a linear model with the logit of sensitivity to disturbance k (S_k) as response variable and the two first axis of the PCA as explanatory variables. This approach minimizes the risk of observing collinearity between explanatory variables, as climatic variables tend to be highly correlated with each other. To account for the uncertainty around the parameters estimated by the bayesian model (eq. 2) in the disturbance sensitivity estimation, we included in each model a weight corresponding to the inverse of the variance of S_k (calculated on logit scale).

Effect of disturbance-related climate indices - We studied the effect of disturbance-related climatic indices (i.e., max wind speed, fire weather index and snow water equivalent) on the logit of sensitivity to the corresponding disturbances (i.e., storm, fire and snow respectively) by fitting three separate linear regressions. We used the same approach to account for the uncertainty around sensitivity (weight calculated as the inverse of the variance on logit scale).

All statistical analyses were conducted with R 4.1.2 (RCoreTeam, 2019). Mixed models were fitted with the "lme4" package (Bates et al., 2014).

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4 Results

4.1 Diameter and dominance effect on disturbance sensitivity

Model validation - For each species-level (*i.e.,* a_0, a_1, b and c in eq. 2) and plot-level (*i.e.,* latent disturbance intensity, referred to as I in eq. 2) parameter, the potential scale reduction statistic (rhat) was systematically lower than 1.1 (supporting information F.1, fig. S3) which indicates a satisfying convergence of the three Markov chains. The predictions were also consistent with the observed death rates (supporting information F.2, fig. S4). We verified that our model was able to disentangle species sensitivity and exposure by showing that species estimated disturbance sensitivity was not related to (i) the mean estimated disturbance intensity in the disturbed plots of that species nor (ii) to the number of trees of each species exposed to the disturbance (see supporting information F.4).

Tree size effect on tree mortality - Tree size, measured by dbh, had a particularly strong effect on fire mortality, with smaller trees being much more fire sensitive (Fig. 2). The effect of dbh on storm mortality was rarely significant (*i.e.,* for 3 species only: *Pinus radiata*, *Pseudotsuga menziesii* and *Fagus sylvatica*), but always positive when it was significant (Fig. 2) - *i.e.,* larger trees were more sensitive to storm. Similarly, tree size had a non-significant effect on snow mortality (Fig. 2). For both biotic and other disturbances, tree size had a significant negative effect on mortality for around half of the species included in the model (the effect being mostly non-significant for the other half) (Fig. 2).

Dominance effect - For both snow and storm mortality, dominance had a mostly negative effect on mortality: dominated trees were thus more likely to be killed by storm or snow (Fig. 2). In the case of storm mortality, this negative dominance effect was particularly strong for conifer species such as *Pinus radiata*, *Pseudotsuga menziesii* or *Pinus pinea*.

Ranking between species - For all disturbance types (especially for storm and biotic disturbances), we observed that the most sensitive species were conifer species (mostly from the genus *Pinus*) while the least sensitive species tended to be broadleaf species (mostly from the genus *Quercus*) (Fig. 2).

4.2 Relation between functional traits and disturbance sensitivity

Effect of traits on sensitivity per disturbance type - We found that species with a high wood density, a low height-to-dbh ratio, a low P50 and a low maximum growth were

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less sensitive to storm disturbances (Fig. 3, supporting information G, table S2). Fire sensitivity was negatively correlated with bark thickness and shade tolerance, and positively correlated with P50 and leaf C/N, while sensitivity to biotic disturbances decreased with species leaf N_{mass} and increased with leaf thickness (Fig. 3, supporting information G, table S2). The effect of traits on snow sensitivity was not shown since the number of individuals for which we could estimate snow sensitivity and collect trait data was insufficient to conduct reliable regressions (but see supporting information G, table S2 for the results).

Effect of traits on sensitivity with broadleaves and conifers treated separately - Most of the trait-sensitivity relation reported above, which were found when all species were included in the model, held true when separating conifer and broadleaf species (supporting information G). The main exceptions were the effect of leaf traits on biotic and fire sensitivity that were not significant anymore (supporting information G). We also found that for conifer species only: storm sensitivity increased with shade tolerance (F = 9.2, p = 0.02) and fire sensitivity decreased with wood density (F = 162.7, p < 0.01) (supporting information G, table S4).

Effect of traits on disturbance sensitivity across all disturbance types - We found that four traits were significantly correlated with the sensitivity when all disturbance types were analysed together. Disturbance sensitivity decreased with increasing wood density, and increased with increasing height-to-dbh ratio, maximum growth and P50 (Fig. 4). Statistics for the other non-significant traits are reported in supporting information H, table S5. Additionally, an analysis of pairwise correlations between species sensitivity to different disturbance types showed that there was in general a positive correlation between species sensitivity to different disturbance type. For instance, species with high sensitivity to biotic disturbance had also high sensitivity to both snow and storm disturbances (supporting information I, fig. S6).

4.3   Effect of species mean climate on disturbance sensitivity

Effect of species mean climate on disturbance sensitivity - The first PCA axis accounted for 77.38% of the variability between species mean climate, and contrasted species from hot and dry climate with species from cold and wet climates (Fig. 5.a). This PCA axis only had a significant negative effect on fire sensitivity (Fig. 5.b): species from hot and dry climates are thus less sensitive to fire. The second PCA axis (20.58% of the variability between species) contrasts species from hot and wet climate against species from cold and dry climates, and was not significantly related to sensitivity when all disturbance types were analyzed together (Fig. 5).

Links between species disturbance exposure and species disturbance sensitivity - We

found that species distributed in fire prone areas (as measured by the fire weather index) are more resistant to fire (Fig. 6). Species mean snow water equivalent and max wind speed were not related to the sensitivity to snow and storm disturbances, respectively (Fig. 6).

5   Discussion

Our study constitutes one of the first attempts to identify species-level drivers of sensitivity to multiple disturbance types at continental scale. We found a high inter-specific variability in disturbance sensitivity that was explained by differences in both functional traits and species mean climate. We found a synergy between the strategies leading to a high resistance to different disturbances, with several traits such as high wood density or low maximum growth leading to high and generic disturbance tolerance.

5.1   Contrasted tree size effects between disturbance types

Negative dbh effect on fire and biotic mortality - Across species, tree size was the strongest driver of mortality from biotic and fire disturbances, with smaller trees being more sensitive. This effect was particularly strong for fire disturbances, and suggests that the negative effect of tree size on fire mortality already observed at local scales (Brando et al., 2012; Trouvé et al., 2021) also holds true at continental scale. This effect is mostly explained by the fact that smaller trees have a thinner bark, making them susceptible even to low intensity ground fire (Catry et al., 2012; Frejaville et al., 2013). Unlike fire, a general consensus on the effect of tree size on biotic-induced tree mortality is lacking, since both the preference of bark beetles or defoliating insects - the main biotic disturbance agents in Europe (Kautz et al., 2017) - and tree response to these agents are highly variable across insect species (Schwilk et al., 2006; Das et al., 2016; Fettig et al., 2019; Koontz et al., 2021). Our finding that overall, biotic disturbances primarily affect smaller trees could be explained by the fact that larger individuals have both higher levels of anti-herbivore defense (Elger et al., 2009) and larger carbon supply to respond to the attack. Larger trees also tend to have a thicker bark which can increase resistance against bark beetles (Valor et al., 2021; Boland and Woodward, 2021). Lastly, as smaller trees are also exposed to a higher competition, this result would be consistent with the concept of cumulative stress developed by Franklin et al. (1987), assuming that tree mortality derives from the accumulation of different stressors (biotic and competition in this case).

Contrasted dbh effect on snow and storm mortality - We found that the effect of tree size on mortality induced by snow and storm was rarely significant but always positive when significant. The small proportion of species for which mortality increases with diameter contrasts with most studies on snow (Nykänen et al., 1997) and storm (Canham et al., 2001, 2010; Díaz-Yáñez et al., 2019) disturbances that consistently found a very strong positive effect of tree size on mortality for nearly all studied species. The assumption that trees with large diameter are more sensitive to storms and snow mostly relies on the positive correlation between tree height and tree

diameter, due to the higher lever arm exerted on the crown of taller trees (Gardiner, 2021). However, larger and older trees also tend to have a more developed rooting system, providing a better anchorage in the soil, and this could partly compensate for the lever arm effect. In addition, most studies on the effect of tree size on mortality included a majority of conifer species (*e.g.,* Canham et al., 2001, 2010; Hale et al., 2012; Gardiner, 2021), which tend to be more sensitive to wind disturbances (Gardiner et al., 2010). The small proportion of species for which the effect of diameter is significant in our study could thus result from the relatively high proportion of broadleaved species (i.e., over 50%). Lastly, the recent study of Jackson et al. (2019) showed that the relation between tree diameter and storm sensitivity may vary due to differences in height-to-dbh ratio among trees, which could explain the fact that the positive relation between tree size and snow and storm mortality was less obvious in our model. We could also assume that following high-intensity windstorms, salvage logging removes all trees in the stand and not only the large ones that were killed. Under this assumption, our choice to count all harvested trees as dead in disturbed plots could blur the effect of diameter on storm mortality.

Dominance effect - Unexpectedly, dominated trees were more sensitive to storm and snow. Dominated trees are expected to be less affected than dominant trees due to the protective effect of dominant trees, and to a decreased height-to-dbh ratio induced by competition (Hale et al., 2012). However, the higher competition experienced by dominated trees could also partly explain our result, as we did not include background mortality in our model and thus did not control for the effect of suppression, that is known to mainly affect relatively smaller trees (Lines et al., 2010; Ruiz-Benito et al., 2013) and that can increase trees susceptibility to disturbances (Hurst et al., 2011; Das et al., 2016). Furthermore, in uneven-aged plots, secondary damage such as the fall of dominant trees over smaller trees could also contribute to explain the high mortality rates observed among dominated trees.

Ranking between species - We found that disturbance sensitivity was highly variable across species for all disturbance types, with a ranking between species that seems to be overall consistent with the literature. For instance, we found that *Picea abies*, known to be particularly sensitive to and affected by bark beetle outbreaks (Hlásny and Turčáni, 2013), was one of the most sensitive species to biotic disturbances, while *Quercus* species were often among the least sensitive species for all disturbance types. Interestingly, economically productive conifer species (e.g., most *Pinus* species, *Picea abies*, *Pseudotsuga menziesii*) were among the most sensitive species. This likely aligns with the commonly observed trade-off between productivity and mortality - *i.e.,* forests with a high productivity also have higher mortality rates (Stephenson et al., 2011; Esquivel-Muelbert et al., 2020). In addition, the higher vulnerability of these species could result from their frequent use in plantations, which tend to be more sensitive than naturally regenerated forests (Morimoto et al., 2019).

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Such plantations can occur outside of species native range, and are often even-aged monocultures, which can for instance be more vulnerable to storm due to the higher wind speed within even-aged stands (Pukkala et al., 2016), or to biotic disturbances by promoting host specific pests (Jactel and Brockerhoff, 2007).

5.2   Functional traits driving disturbance sensitivity

Traits driving specific disturbance types - Our identification of key traits correlated to species disturbance sensitivity is crucial to predict how changing disturbance regimes will affect future forest composition. Our results show that several relations between species traits and disturbance sensitivity already documented in the literature at small spatial scale hold true at continental scale. In particular, our study supports the idea that fire-resistant species have a thicker bark, which protects the vascular cambium from overheating (Brando et al., 2012; Frejaville et al., 2013), while species with a low height to dbh ratio are more resistant to storm and snow disturbances thanks to the lower lever arm exerted on the crown (Jackson et al., 2019). Furthermore, we were able to identify new traits correlated with the sensitivity to each type of disturbance, and these relations were overall consistent with our initial hypotheses (table 1). Storm-resistant species tended to have a denser wood, which makes sense biologically as wood density increases resistance to stem breakage (Chave et al., 2009). Tree species with a high leaf nitrogen content - a trait that generally correlates positively with fast growth and negatively with anti-herbivore defense (Agrawal and Fishbein, 2006) - were less sensitive to biotic disturbances. This finding is consistent with our initial hypothesis, and supports the idea of a trade-off between defence and herbivory tolerance - *i.e.,* trees that invest in a high level of defence are less likely to be attacked but once attacked, they are less able to tolerate herbivory (Herms and Mattson, 1992; Züst and Agrawal, 2017). Lastly, species with a low P50 - i.e., drought-adapted species - were more resistant to fire. Because fire-prone environments like Mediterranean forests also frequently experience drought, both of these stresses likely acted as selective force for speciation, and whether some traits - *e.g.,* serotiny for regeneration - were selected by fire or by drought is still debated (Keeley et al., 2011; Keeley and Pausas, 2022). Our finding provides additional evidence that some traits that are related to drought tolerance also increase fire resistance.

Generic traits explaining sensitivity to multiple disturbances - In this study, we found that it was often the same species that better resisted different types of disturbance. Because studies on inter-specific differences in sensitivity are often focused on one disturbance type (e.g., Canham et al., 2001; Trouvé et al., 2021), whether there are synergies or trade-offs between species sensitivity to different disturbance types was yet to be determined. Our study fills this knowledge gap by showing that the sensitivities to different disturbance types are positively correlated with each other (supporting information I). In addition, we identified several traits that were corre-

lated with species sensitivity across all disturbance types. The most resistant species presented several common characteristics relatively close to those of storm-resistant species - *i.e.,* high wood density, low height-to-dbh ratio, low P50 and low maximum growth. Maximum growth was by far the trait most correlated with sensitivity across all disturbance types, which is consistent with the demographic trade-off between growth and mortality (Esquivel-Muelbert et al., 2020). These characteristics are typical of Mediterranean oaks like *Quercus ilex* or *Quercus suber*, which are already predicted to become more and more widespread in Europe due to their higher drought tolerance (Hanewinkel et al., 2013).

Intra vs inter-specific trait variation - It is noticeable that our results were obtained with a mean trait value per species, without considering intra-specific variability. The relative importance of intra- and inter-specific trait variation tends to differ between traits: traits such as the root mass fraction are largely dominated by inter-specific variability (Poorter et al., 2012) whereas intra-specific variation can explain a significant share of variability between individuals for leaf traits such as the nitrogen content (Auger and Shipley, 2013). Accounting for the intra-specific trait variation could have enabled us to identify additional or stronger relations between functional traits and disturbance sensitivity, but the trait data at the tree-level are often too costly (both in time and resource) to measure in large datasets such as national forest inventories. Nevertheless, the numerous relations between traits and sensitivity that we identified and that were consistent with our initial hypotheses show that species-level trait can strongly contribute to explain disturbance impact on tree mortality.

5.3 Fire sensitivity is driven by species mean climate

Effect of species mean climate - We found evidence that species mean climate influences their sensitivity to disturbances. Previous work linking species climatic niche to their vulnerability to climate change had so far focused on drought mortality, and converge on the idea that species distributed in warmer areas were more drought-tolerant (Zolkos et al., 2015; Rogers et al., 2017). Our study shows that the trend is similar for fire mortality with species from drier and warmer climate being the least sensitive to fire. As evidenced with our trait analysis, this partly derives from the convergence between traits related to drought and to fire (Keeley and Pausas, 2022). For instance, high wood density can limit the spread of wood decay in trees injured (Romero and Bolker, 2008) and increase resistance to xylem cavitation (Pratt et al., 2007; Jacobsen et al., 2007) so that species with high wood density are more adapted both to disturbances such as fire and to drought.

Effect of historical exposition to disturbances - We showed that species distributed in fire prone areas were more resistant to fire disturbances. Though it should be interpreted cautiously as there was a high scatter in species sensitivity to fire around the

regression, this finding aligns well with previous studies showing that fire can act as an evolutionary force to select traits adapted to that disturbance (Keeley et al., 2011; Johnstone et al., 2016). Our findings suggest that resistance and survival through *e.g.,* greater bark thickness are part of these adaptations to fire, along with traits known to promote post-fire resilience such as serotiny, resprouting, smoke-induced germination (Keeley et al., 2011). We did not find such a trend for storms or for snow: the max wind speed or mean snow load in species native distribution was not related to their sensitivity to these two disturbance types. This may partly derives from the fact that these two indices do not characterize the impact of these disturbances as well as would indices quantifying extreme wind speed or snow load anomalies (Suvanto et al., 2021). In addition, fire disturbances had on average a much higher severity and thus a greater potential to act as a selective force for survival as compared to storm or snow that were mostly low-intensity disturbances in our study area (see Fig. 1). Our results are thus consistent with recent studies showing that fire acted as a selective force for many species (Keeley et al., 2011; Keeley and Pausas, 2022), and suggest that fire is a stronger selective force at the species-level compared to storms or snow.

Implications for future forest composition - Recent studies of disturbance dynamics in Europe show that disturbances will become more frequent, diverse, and of stronger magnitude with global changes (Seidl et al., 2011, 2017; Senf and Seidl, 2021a), which will likely contribute to drastic changes in future forest composition. Even at the scale of the study period covered by our data, we were able to observe temporal trends in the frequency of several disturbance types in France and in Spain (supporting information J). Our analysis showed that species that can be classified as conservative (i.e., low maximum growth, high wood density) are more resistant to all disturbance types. As most of the traits associated with high disturbance sensitivity (e.g., low wood density, high maximum growth and height-to-dbh ratio) rather characterize productive species (Malhi et al., 2004; Chave et al., 2009), we could expect changing disturbance regimes to select for conservative species at the expense of productive ones. These results are highly consistent with the recent study of Smith-Martin et al. (2022) in tropical context. Our finding that disturbance-resistant species mostly originate from arid environments (hot and dry climates) also supports studies that predicted increasing dominance of drought-adapted species with climate change (Hanewinkel et al., 2013; Rogers et al., 2017).
The high resistance of drought-adapted species to disturbances highlights the fact that drought events can strongly interact with other disturbance types and amplify the effect of these disturbances on mortality (Anderegg et al., 2015; Csilléry et al., 2017). In the context of climate change, particular attention should be paid to the consequences of increasingly frequent drought events on disturbance-induced tree mortality. More generally, while this study contributes to improving our knowledge of the consequences of single disturbance events on tree mortality, understanding the numerous interactive effects of disturbances on tree mortality will be a major chal-

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lenge to better anticipate the consequences of climate change for forest ecosystems (Seidl et al., 2017).

6 Conclusion

Using an original modeling approach applied on a dataset covering Mediterranean, temperate and boreal forests, our study is to our knowledge the first to provide a ranking of species sensitivity to multiple disturbance types at continental scale. Furthermore, we shed light on key relations between species functional traits, species mean climate, and their sensitivity to disturbances. As climate change is likely to radically change the disturbance regimes across Europe, our results should help forecast how changing disturbance regimes will impact future forest composition.

7 Acknowledgments

8 Data availability statement

Spanish and French NFI are public and available at `https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2_descargas.aspx`, `https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx` and `https://inventaire-forestier.ign.fr/dataifn/data/export_dataifn_2021.zip`. Finnish National Forest Inventory data cannot be made public because of privacy of forest owners and potential legal issues. All analysis were run on protected cluster by NK to ensure data privacy protection. A request to use the Finnish data with the same constraints can be made to KK. The script to fit the mortality model is avalaible at `https://github.com/jbarrere3/SalvageModel/tree/withFinland`. The outputs of the bayesian model (posterior estimation of each parameter) are stored in `https://zenodo.org/record/7603489`. The analyses on the effect of traits and climate on sensitvity based on these outputs can be reproduced via the script available on Github at `https://github.com/jbarrere3/DisturbancePaper`.

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9 Tables

Table 1: Traits used for the analysis, and their expected effects on disturbance sensitivity to fire (F), snow (SN), storm (ST) and biotic (B) disturbances. Unit and source are provided for each trait. The rationale for the expected trait effects are presented in supporting information D and the method to calculate traits from NFI data is presented in supporting information C

| Trait	Unit	Source	Expected effect on disturbance sensitivity
Architectural traits			
Root mass fraction		Guerrero-Ramírez et al. (2021)	Negative (SN, ST, F)
H/dbh ratio	$m.mm^{-1}$	-	Positive (ST, SN)
Bark thickness	mm	Calculated from Spanish NFI	Negative (F, B)
Drought traits			
P50	MPa	López et al. (2013); Martin-StPaul et al. (2017)	Positive (F)
Leaf thickness	mm	-	Negative (F)
Growth-survival trade-off			
Wood density	$g.cm^3$	Chave et al. (2009); Zanne et al. (2009)	Negative (F, SN, ST, B)
Maximum growth	$mm.year^{-1}$	Calculated from NFI	Positive (F, SN, ST, B)
Plant Lifespan	year	TRY (Kattge et al., 2020)	Negative (ST, SN, F, B)
Growth-defense trade-off			
Leaf Nmass	mg.g	-	Negative (B)
Leaf C/N	$g.cm^{-3}$	-	Positive (B)
Shade tolerance			
Shade tolerance		Niinemets and Valladares (2006)	Negative (ST)

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10 Figure captions
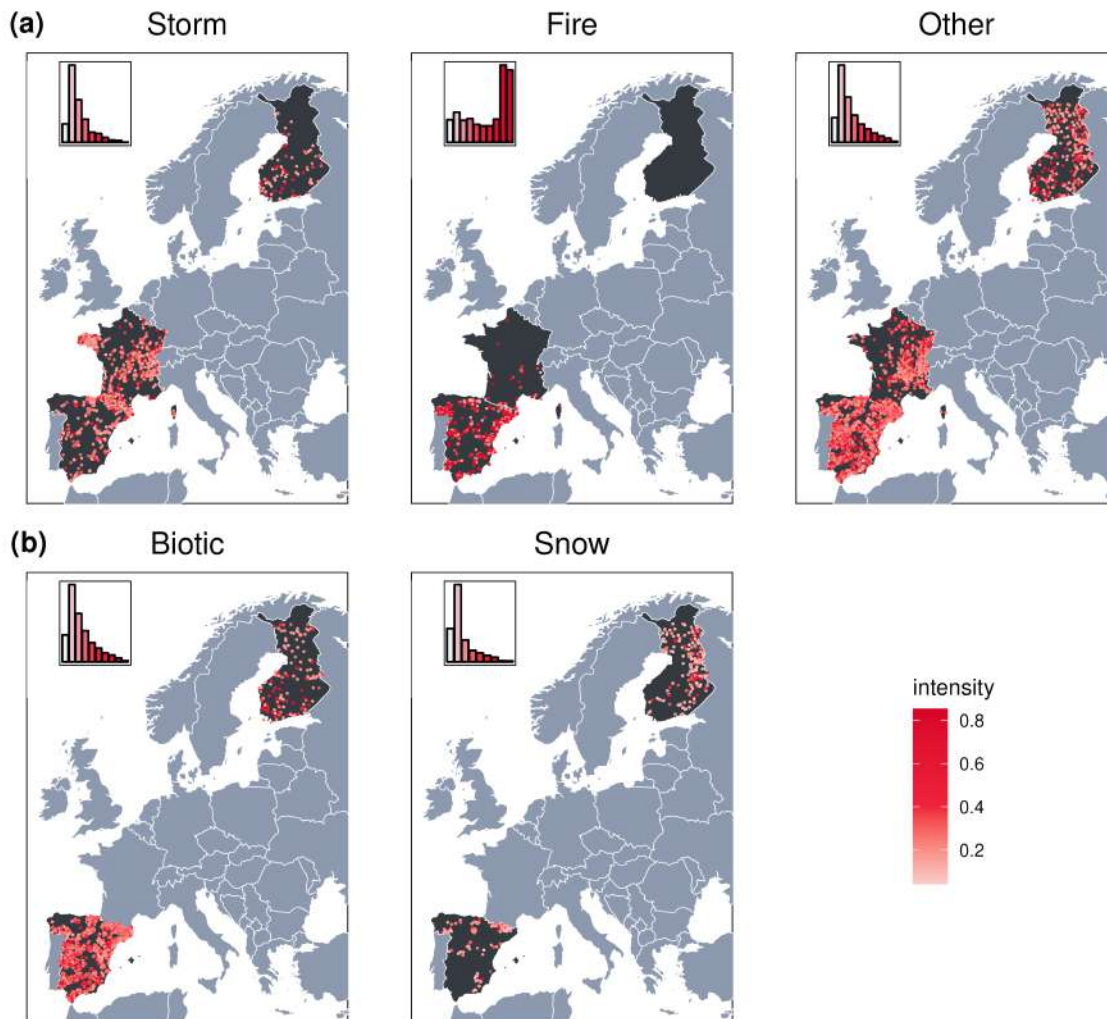
Figure 1: Estimation of the intensity per NFI plot (I_k in eq. 2) of (a) fire, storm and other disturbances in the three countries and of (b) snow and biotic disturbances in Finland and Spain only. The histogram at the topleft corner of each map shows the posterior distribution of disturbance intensity for each disturbance type. Map lines delineate study areas and do not necessarily depict accepted national boundaries
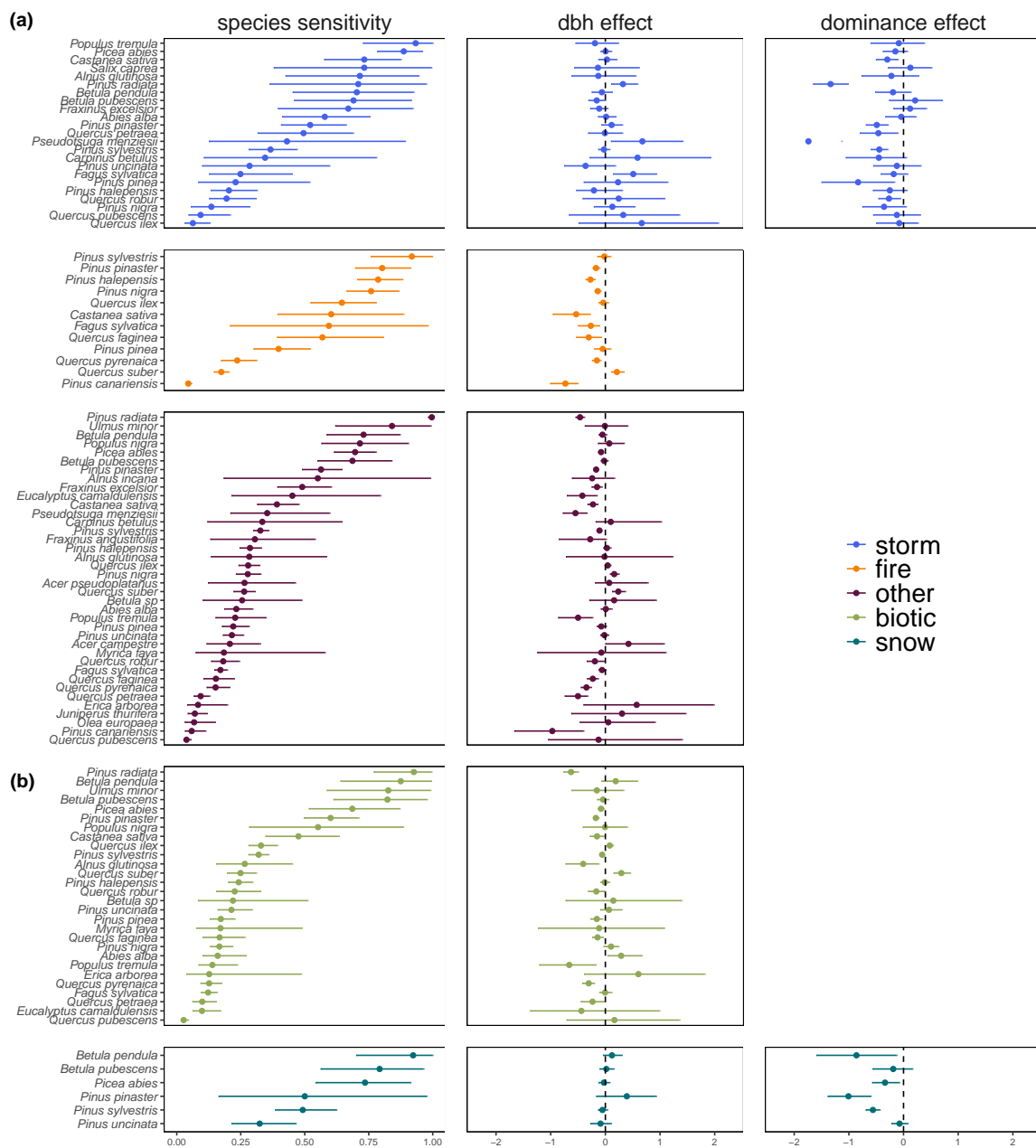
Figure 2: Posterior mean and 95% confidence interval of species sensitivity (eq. 3), and parameters representing dbh effect (c in eq. 2) and dominance effect (a_1 in eq. 2) on mortality for (a) the three disturbance types reported in all the three countries (*i.e.,* fire, storm and other) and (b) the two disturbance types reported in Finland and Spain only (*i.e.,* snow and biotic). Note that dominance effect was only estimated for storm and snow disturbances.
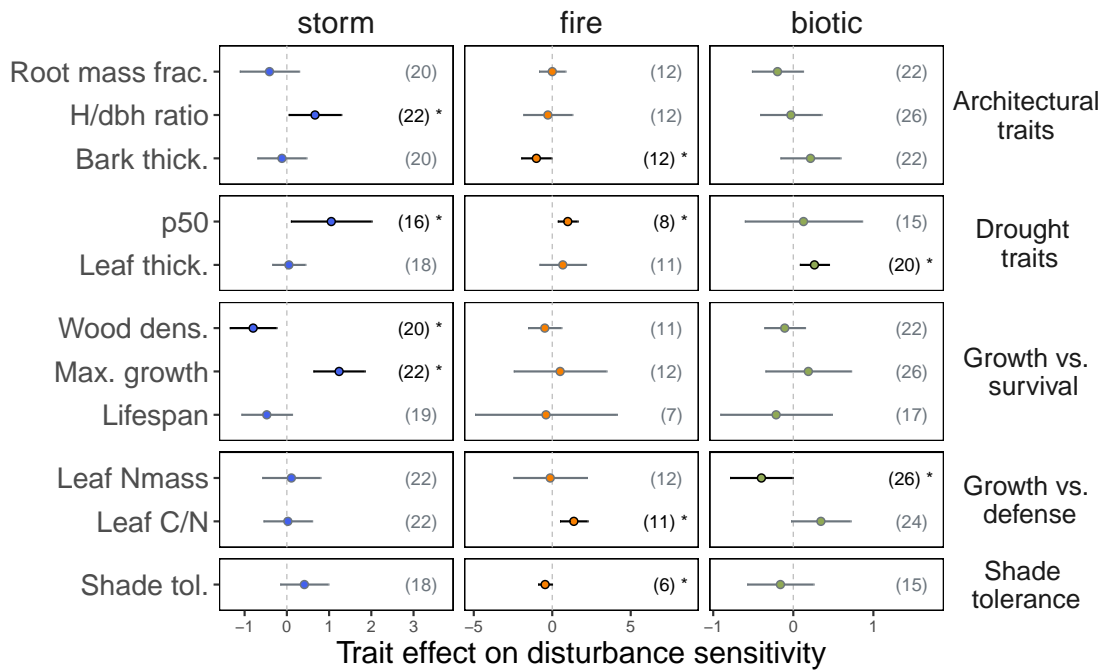
Figure 3: The effects of traits on the sensitivies of trees to storm, fires, and biotic disturbance. Trait values were centered and scale to zero. A negative trait effect means that species with a high value of that trait are more resistant. Error bars represent 95% confidence intervals around the estimate and the numbers in parentheses represent the number of species used in the regression (*i.e.,* species for which we had both an estimation of disturbance sensitivity and a trait value). The symbol * indicates a significant effect of trait on sensitivity at the 5% significance level.
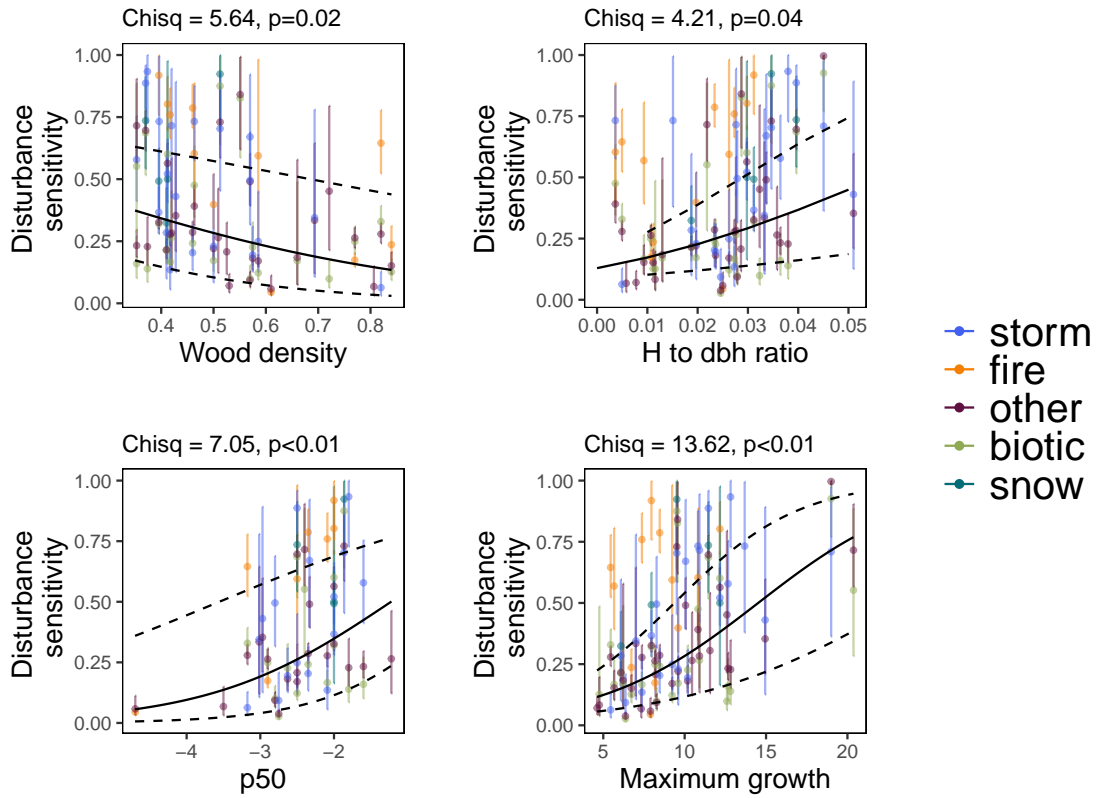
Figure 4: Relation between species sensitivity to disturbance and trait values across all disturbance types. Error bars represents 95% confidence interval around sensitivity, and dashed lines represents 95% confidence interval around the model prediction.
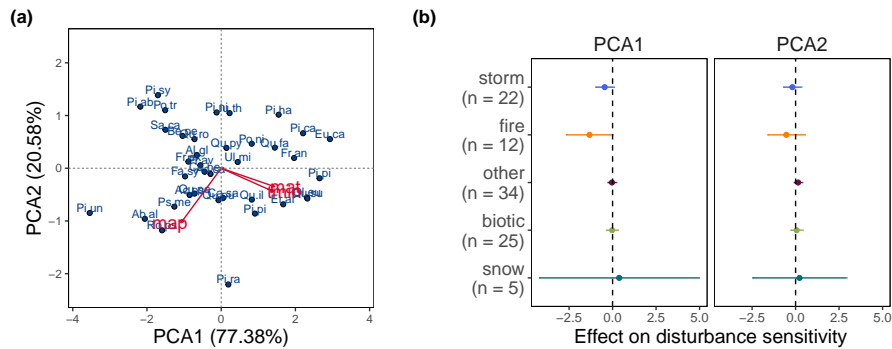

Figure 5: *Relation between species mean climate and disturbance sensitivity.* (a) Principal Component Analysis (PCA) of the three climatic variables to show the position of each species (two first letters of genus and of species) in the climatic space. (b) Estimate of the effect of each PCA axis on disturbance sensitivity. Error bars represent the 95% confidence interval around the estimate.
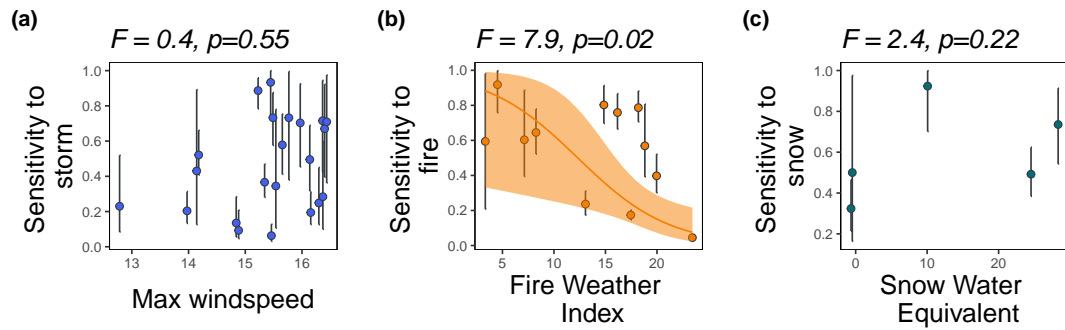
Figure 6: Regressions of species sensitivity against mean disturbance-related climatic indices across specie distribution: (a) max wind speed, (b) fire weather index and (c) snow water equivalent. Error bars represent the 95% confidence interval around disturbance sensitivity. The regression line represents the model prediction (and 95% confidence interval) and is only shown when the effect of the climatic index is significant.