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

4
5 **Running title :** Traits drive tree mortality by disturbances

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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.,

110 2010). In contrast, smaller or thinner trees are in theory more sensitive to fire due
111 to their thinner bark (Michaletz and Johnson, 2007), which is confirmed by several
112 empirical studies that found a strong negative effect of tree size on fire mortality
113 (Brando et al., 2012; Trouvé et al., 2021). Contrary to abiotic agents, the effect of
114 tree size on sensitivity to biotic disturbances is more complex as it strongly depends
115 on the biotic agent (Das et al., 2016; Fettig et al., 2019; Koontz et al., 2021).

116
117 Beyond tree size, inter-specific variations in disturbance sensitivity have also been
118 observed (Canham et al., 2001; Díaz-Yáñez et al., 2019; Trouvé et al., 2021), par-
119 tially attributed to species-level differences in functional traits. Local studies focused
120 on a few species have shown that species with a thick bark and/or denser wood
121 tend to be more resistant to fire (Brando et al., 2012; Catry et al., 2012; Frejaville
122 et al., 2013), and that species with low height to diameter ratio are less susceptible to
123 storms (Gardiner, 2021). But whether these traits effects hold true for all the dom-
124 inant species of a continent, and extend to a broader spectrum of functional traits
125 remain to be determined. In addition to functional traits, inter-specific variation in
126 disturbance sensitivity could also result from differences in the climate and distur-
127 bance regimes experienced by species throughout their evolutionary history. Indeed,
128 recurrent disturbances can exert a strong evolutionary pressure on tree species to
129 select for disturbance adaptive traits (Johnstone et al., 2016). For instance, fire have
130 been documented to select traits facilitating post-disturbance regeneration such as
131 resprouting or serotiny (Keeley et al., 2011; Keeley and Pausas, 2022). Similarly, we
132 could expect tree species to be more resistant to a specific disturbance if they have
133 evolved in areas where this disturbance is frequent. However, whether disturbance
134 regimes have selected species traits promoting resistance strategies following different
135 disturbance types is still unknown.

136
137 Studies that have investigated the drivers of disturbance-induced mortality so far
138 are mostly local and/or focused on a certain type of disturbance. This is mainly due
139 to the difficulty to find disturbance datasets with a sufficiently broad temporal and/or
140 spatial extent. Significant progress is being made on that issue with the analysis of
141 satellite data (Senf and Seidl, 2021a,b), but these data are generally too coarse to
142 identify differences in disturbance-induced mortality between species or individuals.
143 Local studies can bring crucial information on how certain tree-level or stand-level
144 characteristics influence tree susceptibility to a specific disturbance, but their small
145 spatial extent generally makes the comparison of several disturbance types particu-
146 larly difficult. It remains thus unknown whether the effects of tree-level characteristics
147 (e.g., size, dominance) and species traits observed in local studies hold true at con-
148 tinental scale. Furthermore, as forests are exposed to changing disturbance regimes,
149 identifying functional traits predicting consistently species sensitivity to each dis-
150 turbance type would help forecast species response to new disturbance regimes and
151 contribute to improve forest adaptation to climate change. Over the last decades, an

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

156
157 Using NFI data from three countries covering the main climate and disturbance
158 types in Europe (Spain, France and Finland) from 1997 to 2020, we investigated how
159 tree sensitivity to storm, fire, biotic and snow disturbances is influenced by (i) tree
160 size and dominance, (ii) species functional traits, and by (iii) the mean climate in
161 species distribution area.

163 **3 Material and methods**

164 **3.1 Data presentation**

165 **3.1.1 National Forest Inventory data**

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

182
183 In each country, we only considered plots that were measured twice to quantify
184 true mortality events. The time interval between two censuses was systematically 5
185 years in France, and on average 5 and 10 years in Finland and in Spain, respectively
186 (the time interval is not constant for these two countries). The time period and
187 sampling dates covered by each of these three data sets is reported in supporting
188 information A. The plots are circular, with a different sampling radius depending on
189 tree size (see the detailed protocols for each country in supporting information A).

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

208 **3.1.2 Traits data**

209 To investigate how functional traits explain inter-specific differences in disturbance
210 sensitivity, we compiled disturbance-related traits at the species level from various
211 databases - *i.e.*, wood density database (Chave et al., 2009; Zanne et al., 2009),
212 Global Root Traits database (Groot) (Guerrero-Ramírez et al., 2021), shade toler-
213 ance database (Niinemets and Valladares, 2006), P50 databases (Martin-StPaul et al.
214 (2017) and López et al. (2013) for *Pinus canariensis*) and TRY database (Kattge
215 et al., 2020, and see references in supporting information B). We also calculated
216 species-level traits directly from NFI data (*e.g.*, height-to-dbh ratio, bark thickness,
217 maximum growth, see supporting information C for details on the calculation). Traits
218 were selected based on two criteria: relevance regarding the sensitivity to the different
219 disturbances studied, and availability for a sufficient number of species in our dataset.
220 All the traits included in the analysis, their source and the associated hypotheses re-
221 garding disturbance sensitivity are listed in table 1.

222

223 **3.1.3 Climatic data**

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

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

232
233 Similarly, to test if species distributed in areas where a disturbance is frequent are
234 more tolerant to this disturbance, we extracted for each species occurrence obtained
235 from GBIF three disturbance-related climatic indices:

- 236
237 • The Fire Weather Index (FWI) (Vitolo et al., 2020) provides a historical re-
238 construction of meteorological conditions favourable to the start, spread and
239 sustainability of fires at a daily timescale and 28km x 28km spatial resolution.
240 We calculated a species-level FWI as the mean FWI from 2012 to 2021 for each
241 species occurrence point. We chose to only include the last 10 years as the index
242 was spatially consistent between years.
- 243 • To quantify previous wind disturbances over species distribution, we retrieved
244 the hourly wind gust at 10m height at 0am, 3am, 6am, 9am, 12am, 3pm, 6pm
245 and 9pm during the winter months (December to February) over 10 years (from
246 1991 to 2011) from ERA5 database (Hersbach et al., 2018). We computed the
247 95% quantile at each occurrence point, and calculated a species-level max wind
248 speed as the mean 95% quantile value over all occurrence points of a species.
- 249 • We used the Snow Water Equivalent (SWE) (*i.e.*, resulting water column should
250 a snowpack melt in place, calculated based on Takala et al. (2011)), extracted
251 from the GlobSnow database (Luojus et al., 2020), as a proxy for long-term
252 mean snow load conditions. We averaged the mean SWE in winter months
253 from 1979 to 2017 at each species occurrence point to get a species-level SWE.

254 **3.2 Data analysis**

255 **3.2.1 Statistical model**

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

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

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

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

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

284 Where dbh_i is the diameter at breast height (130 cm) of tree i , dqm_j is the mean
 285 quadratic diameter of plot j , $\frac{dbh_i}{dqm_j}$ represents the degree of dominance of tree i in
 286 plot j , I_{jk} is a latent variable ranging between 0 and 1 representing the intensity of
 287 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
 288 for each species s_i and each disturbance k . a_0 corresponds to the intercept, a_1
 289 to the dominance effect, b to the effects of disturbance intensity and dbh, and c to the
 290 direction and magnitude of the dbh effect. Note that $a0_{s_i,k,co_j}$ is also country specific
 291 to account for differences in protocols.

292
 293 Because the dominance status is a driver known to have a strong influence on
 294 storm mortality (Gardiner et al., 2010) and could in theory affect snow mortality but
 295 not specifically the other disturbance types, we have set the value of $a1_{s_i,k}$ to 0 when
 296 $k \neq storm|snow$. For snow and storm, we also tested an alternative model where the
 297 dominance effect was replaced by a stocking effect (*i.e.*, calculated as the cumulative
 298 plot basal area per ha), but we eventually kept the model with dominance since it
 299 had a better DIC than the model with stocking (analysis not shown) and including
 300 both variables would have over-complexified the model.

301

302 Parameters a_0 , a_1 , b and c each followed a normal distribution, with priors cen-
303 tered on 0 and a standard deviation of 100 (except for c that had a prior standard
304 deviation of 1 corresponding to a tighter prior regularization due to its extremely
305 strong effect). The parameter b was restricted to positive values to ensure a positive
306 correlation between the latent variable intensity and mortality risk.

307
308 For the latent variable I_k (intensity of disturbance k), to simplify the complexity
309 of the model and allow the estimation of the distribution, we used a beta distribution,
310 with prior parameters that matched the distribution of disturbance k severity (*i.e.*,
311 severity in a plot affected by disturbance k being defined as the proportion of dead
312 trees in this plot). This approach is slightly different from Trouvé et al. (2021) who
313 used a uniform distribution between 0 and 1, and from Canham et al. (2001, 2010)
314 who estimated the disturbance intensity as fixed parameters and not a latent variable.
315

316 3.2.2 Model fitting

317 We fitted the model separately for each disturbance type. For a given disturbance,
318 parameters in eq. 2 were estimated for a species if this disturbance affected at least
319 15 plots where this species is present, and if the plots affected host at least 150 in-
320 dividuals of that species. Otherwise, individuals of that species were aggregated in
321 "other broadleaf" or "other conifer" (around 10% of the trees included in the model).
322

323 To ensure consistency between the three countries when fitting a model with all
324 countries together, we also included the plots affected by biotic and snow disturbances
325 in Finland and in Spain when fitting the model for the "other" category. Then, to
326 explore the specific response to biotic and snow disturbances, we refitted a model
327 with only Spain and Finland for these two disturbances.
328

329 The models were fitted with a Bayesian framework using the JAGS software
330 (Plummer, 2003) in the R environment (RCoreTeam, 2019). All variables were scaled
331 before fitting the model to a mean of 0 and a standard deviation of 1. We ran three
332 parallel Markov chains with 5000 iterations, a burn-in of 1000 and a thinning rate
333 of 20. We checked convergence by inspecting the chains and checking that Rhat was
334 smaller than 1.1 (see supporting information F).
335

336 3.2.3 Species-specific disturbance sensitivity

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

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

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

351 3.2.4 Relation between traits and disturbance sensitivity

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

361
 362 *Effect of traits on the sensitivity to all disturbance types together* To test whether
 363 some traits could confer resistance to multiple disturbances, we also fitted for each
 364 trait a linear model with as response variable the logit of sensitivity to each distur-
 365 bance types (instead of fitting one model per disturbance type), and the centered and
 366 scaled trait value as explanatory variable. We also added a random species intercept
 367 to account for the multiple observations of sensitivity per species (one species ob-
 368 servation per disturbance type). To account for the uncertainty around disturbance
 369 sensitivity estimation, we included a weight calculated as the inverse of the variance
 370 around disturbance sensitivity.

372 3.2.5 Relation between species mean climate and disturbance sensitivity

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

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

384

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

391

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

394

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

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

441
442 *Effect of traits on sensitivity with broadleaves and conifers treated separately* - Most
443 of the trait-sensitivity relation reported above, which were found when all species were
444 included in the model, held true when separating conifer and broadleaf species (sup-
445 porting information G). The main exceptions were the effect of leaf traits on biotic
446 and fire sensitivity that were not significant anymore (supporting information G).
447 We also found that for conifer species only: storm sensitivity increased with shade
448 tolerance ($F = 9.2$, $p = 0.02$) and fire sensitivity decreased with wood density ($F =$
449 162.7 , $p < 0.01$) (supporting information G, table S4).

450
451 *Effect of traits on disturbance sensitivity across all disturbance types* - We found
452 that four traits were significantly correlated with the sensitivity when all disturbance
453 types were analysed together. Disturbance sensitivity decreased with increasing wood
454 density, and increased with increasing height-to-dbh ratio, maximum growth and P50
455 (Fig. 4). Statistics for the other non-significant traits are reported in supporting
456 information H, table S5. Additionally, an analysis of pairwise correlations between
457 species sensitivity to different disturbance types showed that there was in general
458 a positive correlation between species sensitivity to different disturbance type. For
459 instance, species with high sensitivity to biotic disturbance had also high sensitivity
460 to both snow and storm disturbances (supporting information I, fig. S6).

462 **4.3 Effect of species mean climate on disturbance sensitivity**

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

471
472 *Links between species disturbance exposure and species disturbance sensitivity* - We

473 found that species distributed in fire prone areas (as measured by the fire weather
474 index) are more resistant to fire (Fig. 6). Species mean snow water equivalent and
475 max wind speed were not related to the sensitivity to snow and storm disturbances,
476 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

516 diameter, due to the higher lever arm exerted on the crown of taller trees (Gardiner,
517 2021). However, larger and older trees also tend to have a more developed rooting
518 system, providing a better anchorage in the soil, and this could partly compensate for
519 the lever arm effect. In addition, most studies on the effect of tree size on mortality
520 included a majority of conifer species (*e.g.*, Canham et al., 2001, 2010; Hale et al.,
521 2012; Gardiner, 2021), which tend to be more sensitive to wind disturbances (Gar-
522 diner et al., 2010). The small proportion of species for which the effect of diameter
523 is significant in our study could thus result from the relatively high proportion of
524 broadleaved species (*i.e.*, over 50%). Lastly, the recent study of Jackson et al. (2019)
525 showed that the relation between tree diameter and storm sensitivity may vary due to
526 differences in height-to-dbh ratio among trees, which could explain the fact that the
527 positive relation between tree size and snow and storm mortality was less obvious in
528 our model. We could also assume that following high-intensity windstorms, salvage
529 logging removes all trees in the stand and not only the large ones that were killed.
530 Under this assumption, our choice to count all harvested trees as dead in disturbed
531 plots could blur the effect of diameter on storm mortality.

532
533 *Dominance effect* - Unexpectedly, dominated trees were more sensitive to storm
534 and snow. Dominated trees are expected to be less affected than dominant trees
535 due to the protective effect of dominant trees, and to a decreased height-to-dbh ratio
536 induced by competition (Hale et al., 2012). However, the higher competition experi-
537 enced by dominated trees could also partly explain our result, as we did not include
538 background mortality in our model and thus did not control for the effect of sup-
539 pression, that is known to mainly affect relatively smaller trees (Lines et al., 2010;
540 Ruiz-Benito et al., 2013) and that can increase trees susceptibility to disturbances
541 (Hurst et al., 2011; Das et al., 2016). Furthermore, in uneven-aged plots, secondary
542 damage such as the fall of dominant trees over smaller trees could also contribute to
543 explain the high mortality rates observed among dominated trees.

544
545 *Ranking between species* - We found that disturbance sensitivity was highly vari-
546 able across species for all disturbance types, with a ranking between species that
547 seems to be overall consistent with the literature. For instance, we found that *Picea*
548 *abies*, known to be particularly sensitive to and affected by bark beetle outbreaks
549 (Hlásny and Turčáni, 2013), was one of the most sensitive species to biotic distur-
550 bances, while *Quercus* species were often among the least sensitive species for all
551 disturbance types. Interestingly, economically productive conifer species (*e.g.*, most
552 *Pinus* species, *Picea abies*, *Pseudotsuga menziesii*) were among the most sensitive
553 species. This likely aligns with the commonly observed trade-off between productiv-
554 ity and mortality - *i.e.*, forests with a high productivity also have higher mortality
555 rates (Stephenson et al., 2011; Esquivel-Muelbert et al., 2020). In addition, the higher
556 vulnerability of these species could result from their frequent use in plantations, which
557 tend to be more sensitive than naturally regenerated forests (Morimoto et al., 2019).

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

562 **5.2 Functional traits driving disturbance sensitivity**

563 *Traits driving specific disturbance types* - Our identification of key traits correlated to
564 species disturbance sensitivity is crucial to predict how changing disturbance regimes
565 will affect future forest composition. Our results show that several relations between
566 species traits and disturbance sensitivity already documented in the literature at
567 small spatial scale hold true at continental scale. In particular, our study supports
568 the idea that fire-resistant species have a thicker bark, which protects the vascular
569 cambium from overheating (Brando et al., 2012; Frejaville et al., 2013), while species
570 with a low height to dbh ratio are more resistant to storm and snow disturbances
571 thanks to the lower lever arm exerted on the crown (Jackson et al., 2019). Further-
572 more, we were able to identify new traits correlated with the sensitivity to each type
573 of disturbance, and these relations were overall consistent with our initial hypothe-
574 ses (table 1). Storm-resistant species tended to have a denser wood, which makes
575 sense biologically as wood density increases resistance to stem breakage (Chave et al.,
576 2009). Tree species with a high leaf nitrogen content - a trait that generally correlates
577 positively with fast growth and negatively with anti-herbivore defense (Agrawal and
578 Fishbein, 2006) - were less sensitive to biotic disturbances. This finding is consistent
579 with our initial hypothesis, and supports the idea of a trade-off between defence and
580 herbivory tolerance - *i.e.*, trees that invest in a high level of defence are less likely
581 to be attacked but once attacked, they are less able to tolerate herbivory (Herms
582 and Mattson, 1992; Züst and Agrawal, 2017). Lastly, species with a low P50 - *i.e.*,
583 drought-adapted species - were more resistant to fire. Because fire-prone environ-
584 ments like Mediterranean forests also frequently experience drought, both of these
585 stresses likely acted as selective force for speciation, and whether some traits - *e.g.*,
586 serotiny for regeneration - were selected by fire or by drought is still debated (Keeley
587 et al., 2011; Keeley and Pausas, 2022). Our finding provides additional evidence that
588 some traits that are related to drought tolerance also increase fire resistance.

589
590 *Generic traits explaining sensitivity to multiple disturbances* - In this study, we
591 found that it was often the same species that better resisted different types of distur-
592 bance. Because studies on inter-specific differences in sensitivity are often focused on
593 one disturbance type (*e.g.*, Canham et al., 2001; Trouvé et al., 2021), whether there
594 are synergies or trade-offs between species sensitivity to different disturbance types
595 was yet to be determined. Our study fills this knowledge gap by showing that the
596 sensitivities to different disturbance types are positively correlated with each other
597 (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

638 regression, this finding aligns well with previous studies showing that fire can act as
639 an evolutionary force to select traits adapted to that disturbance (Keeley et al., 2011;
640 Johnstone et al., 2016). Our findings suggest that resistance and survival through *e.g.*,
641 greater bark thickness are part of these adaptations to fire, along with traits known
642 to promote post-fire resilience such as serotiny, resprouting, smoke-induced germination
643 (Keeley et al., 2011). We did not find such a trend for storms or for snow: the
644 max wind speed or mean snow load in species native distribution was not related to
645 their sensitivity to these two disturbance types. This may partly derives from the fact
646 that these two indices do not characterize the impact of these disturbances as well as
647 would indices quantifying extreme wind speed or snow load anomalies (Suvanto et al.,
648 2021). In addition, fire disturbances had on average a much higher severity and thus
649 a greater potential to act as a selective force for survival as compared to storm or
650 snow that were mostly low-intensity disturbances in our study area (see Fig. 1). Our
651 results are thus consistent with recent studies showing that fire acted as a selective
652 force for many species (Keeley et al., 2011; Keeley and Pausas, 2022), and suggest
653 that fire is a stronger selective force at the species-level compared to storms or snow.

654
655 *Implications for future forest composition* - Recent studies of disturbance dynam-
656 ics in Europe show that disturbances will become more frequent, diverse, and of
657 stronger magnitude with global changes (Seidl et al., 2011, 2017; Senf and Seidl,
658 2021a), which will likely contribute to drastic changes in future forest composition.
659 Even at the scale of the study period covered by our data, we were able to observe
660 temporal trends in the frequency of several disturbance types in France and in Spain
661 (supporting information J). Our analysis showed that species that can be classified
662 as conservative (i.e., low maximum growth, high wood density) are more resistant to
663 all disturbance types. As most of the traits associated with high disturbance sensi-
664 tivity (e.g., low wood density, high maximum growth and height-to-dbh ratio) rather
665 characterize productive species (Malhi et al., 2004; Chave et al., 2009), we could ex-
666 pect changing disturbance regimes to select for conservative species at the expense of
667 productive ones. These results are highly consistent with the recent study of Smith-
668 Martin et al. (2022) in tropical context. Our finding that disturbance-resistant species
669 mostly originate from arid environments (hot and dry climates) also supports studies
670 that predicted increasing dominance of drought-adapted species with climate change
671 (Hanewinkel et al., 2013; Rogers et al., 2017).

672 The high resistance of drought-adapted species to disturbances highlights the fact
673 that drought events can strongly interact with other disturbance types and amplify
674 the effect of these disturbances on mortality (Anderegg et al., 2015; Csilléry et al.,
675 2017). In the context of climate change, particular attention should be paid to the
676 consequences of increasingly frequent drought events on disturbance-induced tree mor-
677 tality. More generally, while this study contributes to improving our knowledge of
678 the consequences of single disturbance events on tree mortality, understanding the
679 numerous interactive effects of disturbances on tree mortality will be a major chal-

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

682 **6 Conclusion**

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

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699 **8 Data availability statement**

700 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
706 public because of privacy of forest owners and potential legal issues. All analysis were
707 run on protected cluster by NK to ensure data privacy protection. A request to use
708 the Finnish data with the same constraints can be made to KK. The script to fit the
709 mortality model is available at <https://github.com/jbarrere3/SalvageModel/tree/withFinland>. The outputs of the bayesian model (posterior estimation of each
710 parameter) are stored in <https://zenodo.org/record/7603489>. The analyses on
711 the effect of traits and climate on sensitivity based on these outputs can be reproduced
712 via the script available on Github at <https://github.com/jbarrere3/DisturbancePaper>.
713
714

References

- 715
- 716 Agrawal, A. A. & Fishbein, M. (2006). Plant defense syndromes. *Ecology*, *87*, 132–149
717 <http://www.ncbi.nlm.nih.gov/pubmed/16922309>.
- 718 Allen, C. D., et al. (2010). A global overview of drought and heat-induced tree
719 mortality reveals emerging climate change risks for forests. *Forest Ecology and*
720 *Management*, *259*, 660–684, <https://doi.org/10.1016/j.foreco.2009.09.001>.
- 721 Anderegg, W. R., et al. (2015). Tree mortality from drought, insects, and their
722 interactions in a changing climate. *New Phytologist*, *208*, 674–683, <https://doi.org/10.1111/nph.13477>.
- 724 Auger, S. & Shipley, B. (2013). Inter-specific and intra-specific trait variation along
725 short environmental gradients in an old-growth temperate forest. *Journal of Vege-*
726 *tation Science*, *24*, 419–428, <https://doi.org/10.1111/j.1654-1103.2012.014>
727 [73.x](https://doi.org/10.1111/j.1654-1103.2012.01473.x).
- 728 Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2014). Fitting linear mixed-
729 effects models using lme4. *Journal of Statistical Software*, *67*, 1–51.
- 730 Bauman, D., et al. (2022). Tropical tree mortality has increased with rising atmo-
731 spheric water stress. *Nature*, <https://doi.org/10.1038/s41586-022-04737-7>.
- 732 Boland, J. M. & Woodward, D. L. (2021). Thick bark can protect trees from a severe
733 ambrosia beetle attack. *PeerJ*, *9*, <https://doi.org/10.7717/peerj.10755>.
- 734 Brando, P. M., Nepstad, D. C., Balch, J. K., Bolker, B., Christman, M. C., Coe, M.,
735 & Putz, F. E. (2012). Fire-induced tree mortality in a neotropical forest: The roles
736 of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, *18*,
737 630–641, <https://doi.org/10.1111/j.1365-2486.2011.02533.x>.
- 738 Canham, C. D., Papaik, M. J., & Latty, E. F. (2001). Interspecific variation in
739 susceptibility to windthrow as a function of tree size and storm severity for northern
740 temperate tree species. *Canadian Journal of Forest Research*, *31*, 1–10, <https://doi.org/10.1139/x00-124>.
- 742 Canham, C. D., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2010). Variation in
743 susceptibility to hurricane damage as a function of storm intensity in puerto rican
744 tree species. *Biotropica*, *42*, 87–94, <https://doi.org/10.1111/j.1744-7429.20>
745 [09.00545.x](https://doi.org/10.1111/j.1744-7429.2009.00545.x).
- 746 Catry, F. X., Moreira, F., Pausas, J. G., Fernandes, P. M., Rego, F., Cardillo, E., &
747 Curt, T. (2012). Cork oak vulnerability to fire: The role of bark harvesting, tree
748 characteristics and abiotic factors. *PLoS ONE*, *7*, [https://doi.org/10.1371/jo](https://doi.org/10.1371/journal.pone.0039810)
749 [urnal.pone.0039810](https://doi.org/10.1371/journal.pone.0039810).

- 750 Changenet, A., et al. (2021). Occurrence but not intensity of mortality rises towards
751 the climatic trailing edge of tree species ranges in european forests. *Global Ecology*
752 *and Biogeography*, *30*, 1356–1374, <https://doi.org/10.1111/geb.13301>.
- 753 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E.
754 (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*, 351–
755 366, <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.
- 756 Csilléry, K., Kunstler, G., Courbaud, B., Allard, D., Lassègues, P., Haslinger, K., &
757 Gardiner, B. (2017). Coupled effects of wind-storms and drought on tree mortality
758 across 115 forest stands from the western alps and the jura mountains. *Global*
759 *Change Biology*, *23*, 5092–5107, <https://doi.org/10.1111/gcb.13773>.
- 760 Das, A. J., Stephenson, N. L., & Davis, K. P. (2016). Why do trees die? characterizing
761 the drivers of background tree mortality. *Ecology*, *97*, 2616–2627.
- 762 Díaz-Yáñez, O., Mola-Yudego, B., & González-Olabarria, J. R. (2019). Modelling
763 damage occurrence by snow and wind in forest ecosystems. *Ecological Modelling*,
764 *408*, <https://doi.org/10.1016/j.ecolmodel.2019.108741>.
- 765 Elger, A., Lemoine, D. G., Fenner, M., & Hanley, M. E. (2009). Plant ontogeny
766 and chemical defence : older seedlings are better defended. *Oikos*, *118*, 767–773,
767 <https://doi.org/10.1111/j.1600-0706.2009.17206.x>.
- 768 Esquivel-Muelbert, A., et al. (2020). Tree mode of death and mortality risk factors
769 across amazon forests. *Nature Communications*, *11*, [https://doi.org/10.1038/](https://doi.org/10.1038/s41467-020-18996-3)
770 [s41467-020-18996-3](https://doi.org/10.1038/s41467-020-18996-3).
- 771 Fettig, C. J., Mortenson, L. A., Bulaon, B. M., & Foulk, P. B. (2019). Tree mortality
772 following drought in the central and southern sierra nevada, california, u.s. *Forest*
773 *Ecology and Management*, *432*, 164–178, [https://doi.org/10.1016/j.foreco.2](https://doi.org/10.1016/j.foreco.2018.09.006)
774 [018.09.006](https://doi.org/10.1016/j.foreco.2018.09.006).
- 775 Flemons, P., Guralnick, R., Krieger, J., Ranipeta, A., & Neufeld, D. (2007). A
776 web-based gis tool for exploring the world’s biodiversity: The global biodiversity
777 information facility mapping and analysis portal application (gbif-mapa). *Ecological*
778 *Informatics*, *2*, 49–60, <https://doi.org/10.1016/j.ecoinf.2007.03.004>.
- 779 Franklin, J. F., Shugart, H. H., & Harmon, M. E. (1987). Tree death as an ecological
780 process. *BioScience*, *37*, 550–556.
- 781 Frejaville, T., Curt, T., & Carcaillet, C. (2013). Bark flammability as a fire-response
782 trait for subalpine trees. *Frontiers in Plant Science*, *4*, 1–8, [https://doi.org/10](https://doi.org/10.3389/fpls.2013.00466)
783 [.3389/fpls.2013.00466](https://doi.org/10.3389/fpls.2013.00466).

- 784 Gardiner, B. (2021). Wind damage to forests and trees: a review with an emphasis
785 on planted and managed forests. *Journal of Forest Research*, 26, 248–266, <https://doi.org/10.1080/13416979.2021.1940665>.
786
- 787 Gardiner, B., et al. (2010). Destructive storms in european forests: past and forth-
788 coming impacts <https://hal.inrae.fr/hal-02824530>.
- 789 GBIF.org (2022). Gbif occurrence download <https://doi.org/10.15468/dl.ekqs8c>.
- 790 Guerrero-Ramírez, N. R., et al. (2021). Global root traits (groot) database. *Global*
791 *Ecology and Biogeography*, 30, 25–37, <https://doi.org/10.1111/geb.13179>.
- 792 Hale, S. E., Gardiner, B. A., Wellpott, A., Nicoll, B. C., & Achim, A. (2012). Wind
793 loading of trees: Influence of tree size and competition. *European Journal of Forest*
794 *Research*, 131, 203–217, <https://doi.org/10.1007/s10342-010-0448-2>.
- 795 Halofsky, J. E., Peterson, D. L., & Harvey, B. J. (2020). Changing wildfire, changing
796 forests: the effects of climate change on fire regimes and vegetation in the pacific
797 northwest, usa.
- 798 Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J., & Zimmermann,
799 N. E. (2013). Climate change may cause severe loss in the economic value of
800 european forest land. *Nature Climate Change*, 3, 203–207, [https://doi.org/10](https://doi.org/10.1038/nclimate1687)
801 [.1038/nclimate1687](https://doi.org/10.1038/nclimate1687).
- 802 Hember, R. A., Kurz, W. A., & Coops, N. C. (2017). Relationships between
803 individual-tree mortality and water-balance variables indicate positive trends in
804 water stress-induced tree mortality across north america. *Global Change Biology*,
805 23, 1691–1710, <https://doi.org/10.1111/gcb.13428>.
- 806 Herms, D. A. & Mattson, W. J. (1992). The dilemma of plants : to grow or defend.
807 *The Quarterly review of biology*, 67, 283–335.
- 808 Hersbach, H., et al. (2018). Era5 hourly data on single levels from 1959 to present.
809 copernicus climate change service (c3s) climate data store (cds).
- 810 Hlásny, T. & Turčáni, M. (2013). Persisting bark beetle outbreak indicates the un-
811 sustainability of secondary norway spruce forests: Case study from central europe.
812 *Annals of Forest Science*, 70, 481–491, <https://doi.org/10.1007/s13595-013-0>
813 [279-7](https://doi.org/10.1007/s13595-013-0279-7).
- 814 Hurst, J. M., Allen, R. B., Coomes, D. A., & Duncan, R. P. (2011). Size-specific
815 tree mortality varies with neighbourhood crowding and disturbance in a montane
816 nothofagus forest. *PLoS ONE*, 6, [https://doi.org/10.1371/journal.pone.002](https://doi.org/10.1371/journal.pone.0026670)
817 [6670](https://doi.org/10.1371/journal.pone.0026670).

- 818 Jackson, T., et al. (2019). A new architectural perspective on wind damage in a
819 natural forest. *Frontiers in Forests and Global Change*, *1*, <https://doi.org/10.3389/ffgc.2018.00013>.
820
- 821 Jacobsen, A. L., Pratt, R. B., Ewers, F. W., & Davis, S. D. (2007). Cavitation
822 resistance among 26 chaparral species of southern California. *Ecological Monographs*,
823 *77*, 99–115.
- 824 Jactel, H. & Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest
825 insects. *Ecology Letters*, *10*, 835–848, <https://doi.org/10.1111/j.1461-0248.2007.01073.x>.
826
- 827 Johnstone, J. F., et al. (2016). Changing disturbance regimes, ecological memory, and
828 forest resilience. *Frontiers in Ecology and the Environment*, *14*, 369–378, <https://doi.org/10.1002/fee.1311>.
829
- 830 Karger, D. N., et al. (2018). Data from: Climatologies at high resolution for the
831 earth’s land surface areas.
- 832 Karger, D. N., et al. (2017). Climatologies at high resolution for the earth’s land
833 surface areas. *Scientific Data*, *4*, 1–20, <https://doi.org/10.1038/sdata.2017.122>.
834
- 835 Kattge, J., et al. (2020). Try plant trait database – enhanced coverage and open access.
836 *Global Change Biology*, *26*, 119–188, <https://doi.org/10.1111/gcb.14904>.
- 837 Kautz, M., Meddens, A. J., Hall, R. J., & Arneeth, A. (2017). Biotic disturbances in
838 northern hemisphere forests – a synthesis of recent data, uncertainties and impli-
839 cations for forest monitoring and modelling. *Global Ecology and Biogeography*, *26*,
840 533–552, <https://doi.org/10.1111/geb.12558>.
- 841 Keeley, J. E. & Pausas, J. G. (2022). Evolutionary ecology of fire. *Annual Review of*
842 *Ecology, Evolution, and Systematics*, *53*, 10.1–10.23, <https://doi.org/10.1146/annurev-ecolsys-102320> <https://doi.org/10.1146/annurev-ecolsys-102320>
843
844 20–.
- 845 Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011).
846 Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*,
847 406–411.
- 848 Koontz, M. J., Latimer, A. M., Mortenson, L. A., Fettig, C. J., & North, M. P.
849 (2021). Cross-scale interaction of host tree size and climatic water deficit governs
850 bark beetle-induced tree mortality. *Nature Communications*, *12*, <https://doi.org/10.1038/s41467-020-20455-y>.
851

- 852 Kulha, N., Pasanen, L., Holmström, L., Grandpré, L. D., Gauthier, S., Kuuluvainen,
853 T., & Aakala, T. (2020). The structure of boreal old-growth forests changes at
854 multiple spatial scales over decades. *Landscape Ecology*, *35*, 843–858, <https://doi.org/10.1007/s10980-020-00979-w>.
855
- 856 Kunstler, G., et al. (2020). Demographic performance of european tree species at
857 their hot and cold climatic edges. *Journal of Ecology*, (pp. 1–14)., <https://doi.org/10.1111/1365-2745.13533>.
858
- 859 Lines, E. R., Coomes, D. A., & Purves, D. W. (2010). Influences of forest structure,
860 climate and species composition on tree mortality across the eastern us. *PLoS*
861 *ONE*, *5*, <https://doi.org/10.1371/journal.pone.0013212>.
- 862 Luoju, K., Pullianen, J., Takala, M., Lemmetyinen, J., & Moisander, M. (2020).
863 Globsnow v3.0 snow water equivalent (swe). *PANGAEA*.
- 864 López, R., Heredia, U. L. D., Collada, C., Cano, F. J., Emerson, B. C., Cochard,
865 H., & Gil, L. (2013). Vulnerability to cavitation, hydraulic efficiency, growth and
866 survival in an insular pine (*pinus canariensis*). *Annals of Botany*, *111*, 1167–1179,
867 <https://doi.org/10.1093/aob/mct084>.
- 868 Malhi, Y., et al. (2004). The above-ground coarse wood productivity of 104 neotropical
869 forest plots. *Global Change Biology*, *10*, 563–591, <https://doi.org/10.1111/j.1529-8817.2003.00778.x>.
870
- 871 Martin-StPaul, N., Delzon, S., & Cochard, H. (2017). Sureau database : A database
872 of hydraulic and stomatal traits for modelling drought resistance in plants [data
873 set].
- 874 McDowell, N. G., et al. (2020). Pervasive shifts in forest dynamics in a changing
875 world. *Science*, *368*, <https://doi.org/10.1126/science.aaz9463>.
- 876 Michaletz, S. T. & Johnson, E. A. (2007). How forest fires kill trees: A review of the
877 fundamental biophysical processes. volume 22 (pp. 500–515).
- 878 Morimoto, J., et al. (2019). Comparison of vulnerability to catastrophic wind between
879 abies plantation forests and natural mixed forests in northern japan. *Forestry*, *92*,
880 436–443, <https://doi.org/10.1093/forestry/cpy045>.
- 881 Neumann, M., Mues, V., Moreno, A., Hasenauer, H., & Seidl, R. (2017). Climate
882 variability drives recent tree mortality in europe. *Global Change Biology*, *23*, 4788–
883 4797, <https://doi.org/10.1111/gcb.13724>.
- 884 Niinemets, U. & Valladares, F. (2006). Tolerance to shade, drought and waterlogging
885 of temperate northern hemisphere trees and shrubs. *Ecological Monographs*, *76*,
886 521–547 <http://mobot.mobot.org/W3T/Search/foc.html>.

- 887 Nykänen, M.-L., Peltola, H., Quine, C., Kellomäki, S., & Broadgate, M. (1997). Fac-
888 tors affecting snow damage of trees with particular reference to european conditions.
889 *Silva Fennica*, 31, 193–213.
- 890 Plummer, M. (2003). : Jags : A program for analysis of bayesian graphical models
891 using gibbs sampling jags : Just another gibbs sampler. (pp.10). [http://www.ci](http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Proceedings/)
892 [.tuwien.ac.at/Conferences/DSC-2003/Proceedings/](http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Proceedings/).
- 893 Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012).
894 Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific vari-
895 ation and environmental control.
- 896 Pratt, R. B., Jacobsen, A. L., Ewers, F. W., & Davis, S. D. (2007). Relation-
897 ships among xylem transport, biomechanics and storage in stems and roots of
898 nine rhamnaceae species of the california chaparral. *New Phytologist*, 174, 787–798,
899 <https://doi.org/10.1111/j.1469-8137.2007.02061.x>.
- 900 Pukkala, T., Laiho, O., & Lähde, E. (2016). Continuous cover management reduces
901 wind damage. *Forest Ecology and Management*, 372, 120–127, [https://doi.org/](https://doi.org/10.1016/j.foreco.2016.04.014)
902 [10.1016/j.foreco.2016.04.014](https://doi.org/10.1016/j.foreco.2016.04.014).
- 903 RCoreTeam (2019). R: A language and environment for statistical computing. *Vienna,*
904 *Austria*.
- 905 Rogers, B. M., Jantz, P., & Goetz, S. J. (2017). Vulnerability of eastern us tree species
906 to climate change. *Global Change Biology*, 23, 3302–3320, [https://doi.org/10.1](https://doi.org/10.1111/gcb.13585)
907 [111/gcb.13585](https://doi.org/10.1111/gcb.13585).
- 908 Romero, C. & Bolker, B. M. (2008). Effects of stem anatomical and structural traits
909 on responses to stem damage: An experimental study in the bolivian amazon.
910 *Canadian Journal of Forest Research*, 38, 611–618, [https://doi.org/10.1139/](https://doi.org/10.1139/X07-205)
911 [X07-205](https://doi.org/10.1139/X07-205).
- 912 Ruiz-Benito, P., Lines, E. R., Gómez-Aparicio, L., Zavala, M. A., & Coomes, D. A.
913 (2013). Patterns and drivers of tree mortality in iberian forests: Climatic effects
914 are modified by competition. *PLoS ONE*, 8, [https://doi.org/10.1371/journal](https://doi.org/10.1371/journal.pone.0056843)
915 [l.pone.0056843](https://doi.org/10.1371/journal.pone.0056843).
- 916 Schelhaas, M.-J., Nabuurs, G.-J., & Schuck, A. (2003). Natural disturbances in the
917 european forests in the 19th and 20th centuries. *Global Change Biology*, 9, 1620–
918 1633.
- 919 Schwilk, D. W., Knapp, E. E., Ferrenberg, S. M., Keeley, J. E., & Caprio, A. C. (2006).
920 Tree mortality from fire and bark beetles following early and late season prescribed
921 fires in a sierra nevada mixed-conifer forest. *Forest Ecology and Management*, 232,
922 36–45, <https://doi.org/10.1016/j.foreco.2006.05.036>.

- 923 Seidl, R., et al. (2020). Globally consistent climate sensitivity of natural disturbances
924 across boreal and temperate forest ecosystems. *Ecography*, *43*, 967–978, <https://doi.org/10.1111/ecog.04995>.
925
- 926 Seidl, R., Schelhaas, M. J., & Lexer, M. J. (2011). Unraveling the drivers of intensi-
927 fying forest disturbance regimes in europe. *Global Change Biology*, *17*, 2842–2852,
928 <https://doi.org/10.1111/j.1365-2486.2011.02452.x>.
- 929 Seidl, R., et al. (2017). Forest disturbances under climate change. *Nature Climate*
930 *Change*, *7*, 395–402, <https://doi.org/10.1038/nclimate3303> [http://dx.doi](http://dx.doi.org/10.1038/nclimate3303)
931 [.org/10.1038/nclimate3303](http://dx.doi.org/10.1038/nclimate3303).
- 932 Seneviratne, S. I., et al. (2021). Weather and climate extreme events in a changing
933 climate.
- 934 Senf, C., et al. (2018). Canopy mortality has doubled in europe’s temperate forests
935 over the last three decades. *Nature Communications*, *9*, 1–8, [https://doi.org/](https://doi.org/10.1038/s41467-018-07539-6)
936 [10.1038/s41467-018-07539-6](https://doi.org/10.1038/s41467-018-07539-6).
- 937 Senf, C. & Seidl, R. (2021a). Mapping the forest disturbance regimes of europe.
938 *Nature Sustainability*, *4*, 63–70, <https://doi.org/10.1038/s41893-020-00609-y>
939 <http://dx.doi.org/10.1038/s41893-020-00609-y>.
- 940 Senf, C. & Seidl, R. (2021b). Post-disturbance canopy recovery and the resilience of
941 europe’s forests. *Global Ecology and Biogeography*, (pp. 1–12)., [https://doi.org/](https://doi.org/10.1111/geb.13406)
942 [10.1111/geb.13406](https://doi.org/10.1111/geb.13406).
- 943 Smith-Martin, C. M., et al. (2022). Hurricanes increase tropical forest vulnerability
944 to drought. *New Phytologist*, *235*, 1005–1017, [https://doi.org/10.1111/nph.18](https://doi.org/10.1111/nph.18175)
945 [175](https://doi.org/10.1111/nph.18175).
- 946 Stephenson, N. L., et al. (2011). Causes and implications of the correlation between
947 forest productivity and tree mortality rates. *Ecological Monographs*, *81*, 527–555.
- 948 Suvanto, S., Lehtonen, A., Nevalainen, S., Lehtonen, I., Viiri, H., Strandström, M.,
949 & Peltoniemi, M. (2021). Mapping the probability of forest snow disturbances in
950 finland. *Plos One*, *16*, <https://doi.org/10.1371/journal.pone.0254876>.
- 951 Suvanto, S., Peltoniemi, M., Tuominen, S., Strandström, M., & Lehtonen, A. (2019).
952 High-resolution mapping of forest vulnerability to wind for disturbance-aware
953 forestry. *Forest Ecology and Management*, *453*, [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.foreco.2019.117619)
954 [foreco.2019.117619](https://doi.org/10.1016/j.foreco.2019.117619).
- 955 Taccoen, A., et al. (2019). Background mortality drivers of european tree species:
956 Climate change matters. *Proceedings of the Royal Society B: Biological Sciences*,
957 *286*, <https://doi.org/10.1098/rspb.2019.0386>.

- 958 Takala, M., et al. (2011). Estimating northern hemisphere snow water equivalent for
959 climate research through assimilation of space-borne radiometer data and ground-
960 based measurements. *Remote Sensing of Environment*, 115, 3517–3529, <https://doi.org/10.1016/j.rse.2011.08.014>.
961
- 962 Thom, D. & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and
963 biodiversity in temperate and boreal forests. *Biological reviews of the Cambridge*
964 *Philosophical Society*, 91, 760–781, <https://doi.org/10.1111/brv.12193>.
- 965 Trouvé, R., Osborne, L., & Baker, P. J. (2021). The effect of species, size, and fire
966 intensity on tree mortality within a catastrophic bushfire complex. *Ecological Ap-*
967 *plications*, 31, <https://doi.org/10.1002/eap.2383>.
- 968 Valor, T., Hood, S. M., Piqué, M., Larrañaga, A., & Casals, P. (2021). Resin ducts
969 and bark thickness influence pine resistance to bark beetles after prescribed fire.
970 *Forest Ecology and Management*, 494, <https://doi.org/10.1016/j.foreco.2021.119322>.
971
- 972 Vitolo, C., Giuseppe, F. D., Barnard, C., Coughlan, R., San-Miguel-Ayanz, J., Lib-
973 ertá, G., & Krzeminski, B. (2020). Era5-based global meteorological wildfire danger
974 maps. *Scientific Data*, 7, <https://doi.org/10.1038/s41597-020-0554-z>.
- 975 Weed, A. S., Ayres, M. P., & Hicke, J. A. (2013). Consequences of climate change for
976 biotic disturbances in north american forests. *Ecological Monographs*, 83, 441–470.
- 977 Xu, X., Jia, G., Zhang, X., Riley, W. J., & Xue, Y. (2020). Climate regime shift and
978 forest loss amplify fire in amazonian forests. *Global Change Biology*, 26, 5874–5885,
979 <https://doi.org/10.1111/gcb.15279>.
- 980 Yi, C., Hendrey, G., Niu, S., McDowell, N., & Allen, C. D. (2022). Tree mortality
981 in a warming world: Causes, patterns, and implications. *Environmental Research*
982 *Letters*, 17, <https://doi.org/10.1088/1748-9326/ac507b>.
- 983 Zanne, A. E., et al. (2009). Data from: Towards a worldwide wood economics spec-
984 trum. *Dryad Dataset*, <https://doi.org/https://doi.org/10.5061/dryad.234>.
- 985 Zolkos, S. G., Jantz, P., Cormier, T., Iverson, L. R., McKenney, D. W., & Goetz, S. J.
986 (2015). Projected tree species redistribution under climate change: Implications
987 for ecosystem vulnerability across protected areas in the eastern united states.
988 *Ecosystems*, 18, 202–220, <https://doi.org/10.1007/s10021-014-9822-0>.
- 989 Züst, T. & Agrawal, A. A. (2017). Trade-offs between plant growth and defense
990 against insect herbivory: An emerging mechanistic synthesis. *Annual Review of*
991 *Plant Biology*, 68, 513–534, [https://doi.org/10.1146/annurev-arplant-0429](https://doi.org/10.1146/annurev-arplant-042916-040856)
992 [16-040856](https://doi.org/10.1146/annurev-arplant-042916-040856).

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
<i>Architectural traits</i>			
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)
<i>Drought traits</i>			
P50	MPa	López et al. (2013); Martin-StPaul et al. (2017)	Positive (F)
Leaf thickness	mm	-	Negative (F)
<i>Growth-survival trade-off</i>			
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)
<i>Growth-defense trade-off</i>			
Leaf Nmass	mg.g	-	Negative (B)
Leaf C/N	g.cm ⁻³	-	Positive (B)
<i>Shade tolerance</i>			
Shade tolerance		Niinemets and Valladares (2006)	Negative (ST)

994 10 Figure captions

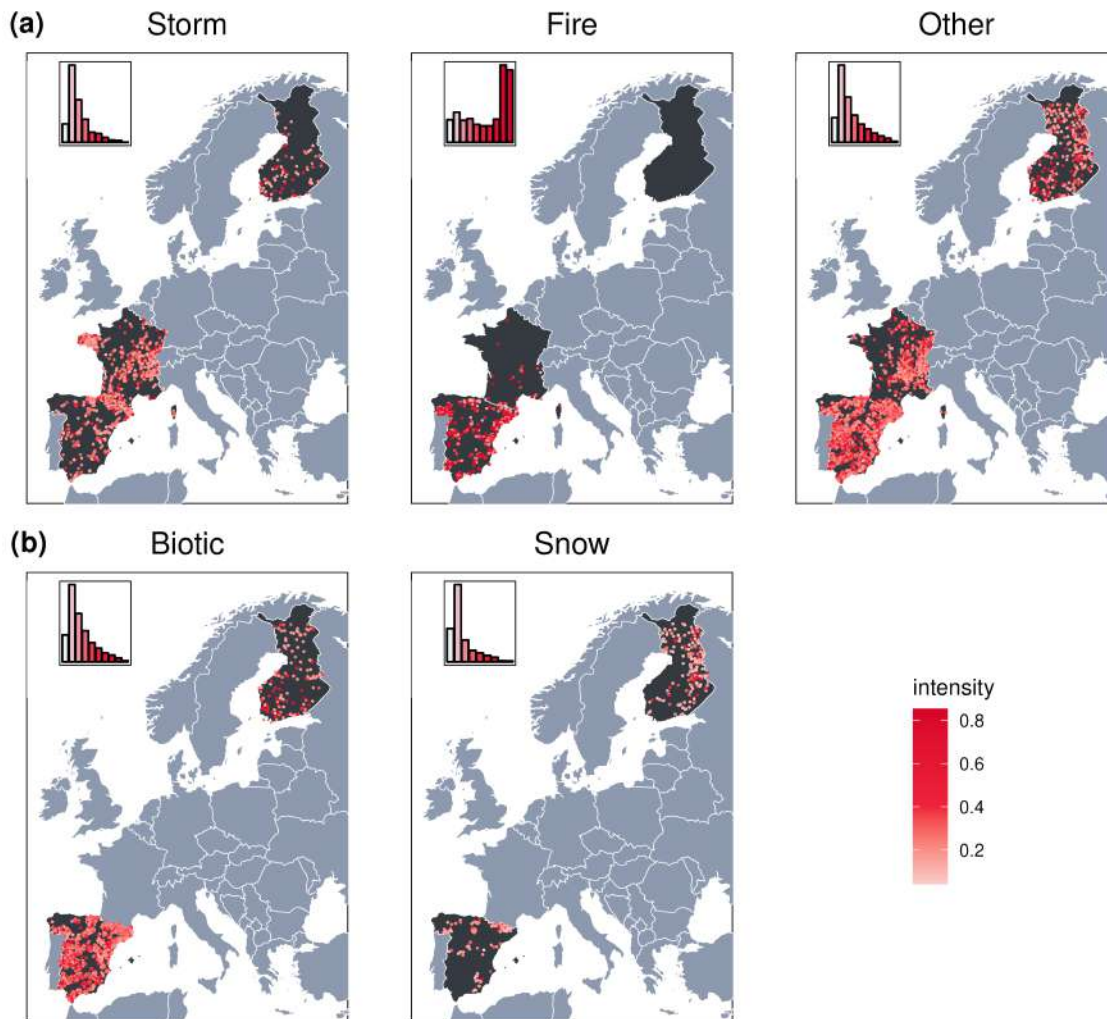


Figure 1: Estimation of the intensity per NFI plot (I_k in eq. 2) of (a) fire, storm and other disturbances in the three countries and of (b) snow and biotic disturbances in Finland and Spain only. The histogram at the topleft corner of each map shows the posterior distribution of disturbance intensity for each disturbance type. Map lines delineate study areas and do not necessarily depict accepted national boundaries

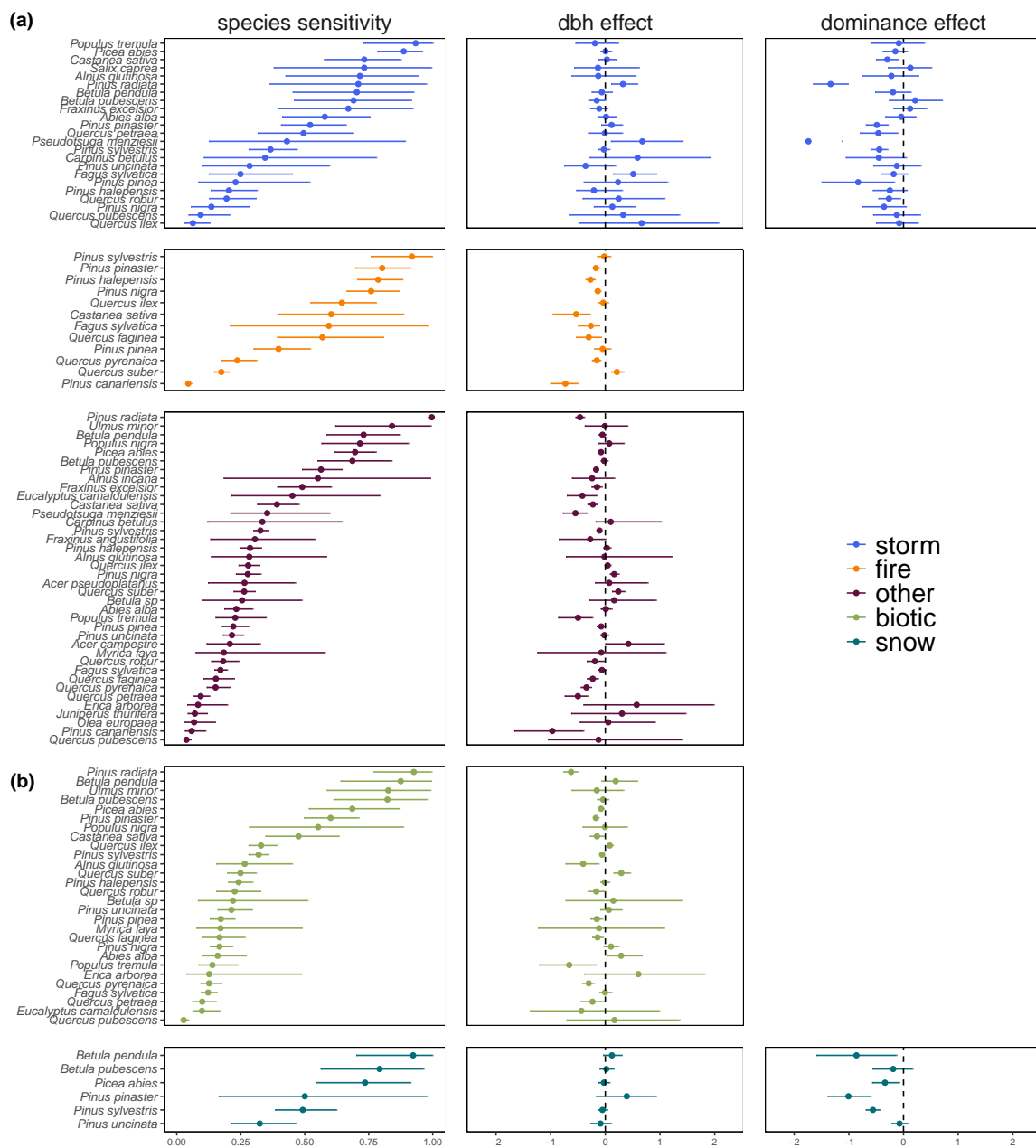


Figure 2: Posterior mean and 95% confidence interval of species sensitivity (eq. 3), and parameters representing dbh effect (c in eq. 2) and dominance effect (a_1 in eq. 2) on mortality for (a) the three disturbance types reported in all the three countries (*i.e.*, fire, storm and other) and (b) the 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.

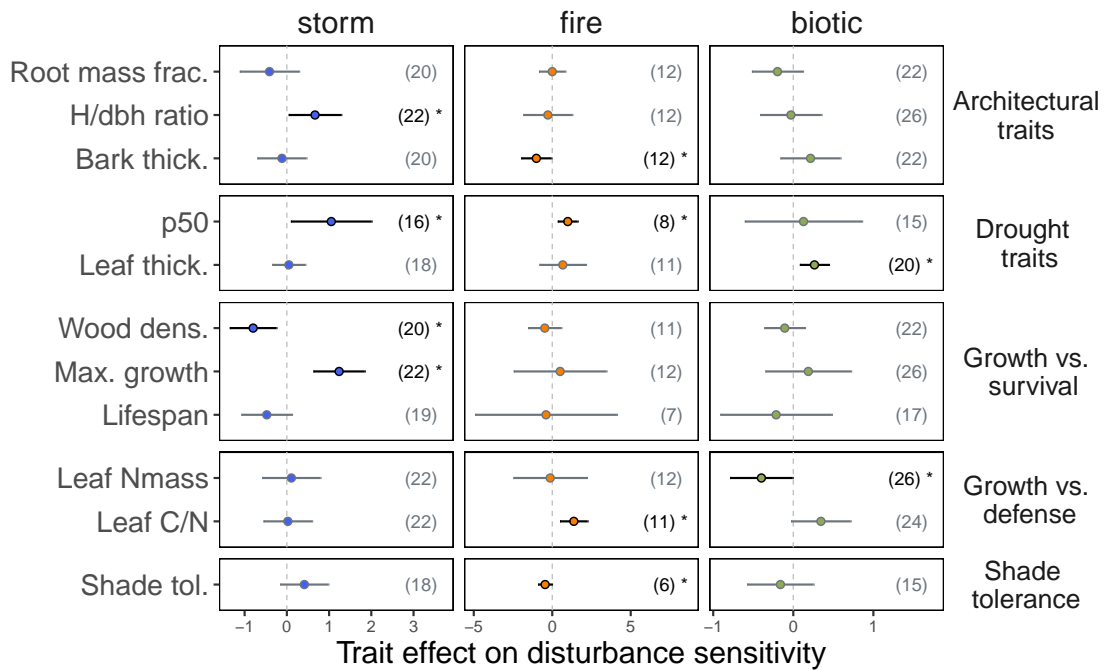


Figure 3: The effects of traits on the sensitivities of trees to storm, fires, and biotic disturbance. Trait values were centered and scale to zero. A negative trait effect means that species with a high value of that trait are more resistant. Error bars represent 95% confidence intervals around the 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.

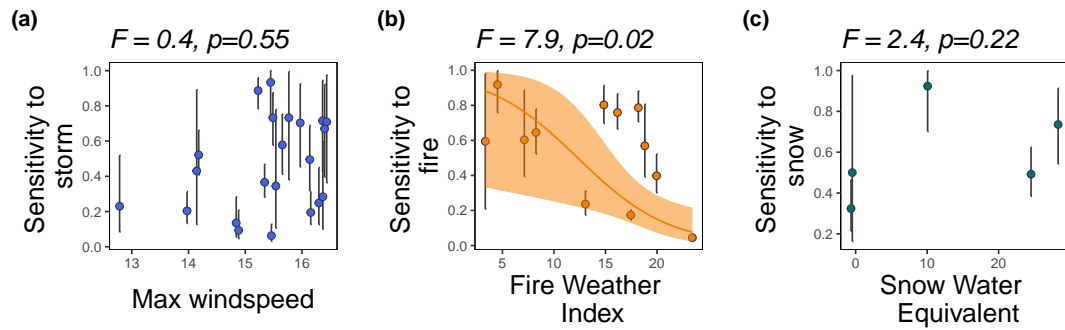


Figure 6: Regressions of species sensitivity against mean disturbance-related climatic indices across specie distribution: (a) max wind speed, (b) fire weather index and (c) snow water equivalent. Error bars represent the 95% confidence interval around disturbance sensitivity. The regression line represents the model prediction (and 95% confidence interval) and is only shown when the effect of the climatic index is significant.