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1 Forest storm resilience depends on the  
2 interplay between functional composition and  
3 climate - insights from European-scale  
4 simulations

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9

# 1 Abstract

1. Tree species composition is known to influence forest productivity, but its effect on forest resilience to disturbances such as storms remains largely unexplored. Furthermore, climate is likely to influence forest resilience directly but also to influence the effect of tree species composition on resilience. In Europe, storm-induced tree mortality is currently increasing across all climatic biomes. Understanding the drivers of forest resilience to storms and its consistency across climates appears to be crucial for predicting the consequences of climate change for European forests.

2. In this study, we used a simulation approach with an integral projection model calibrated with National Forest Inventory (NFI) data at the European scale. We restricted our simulations to tree species assemblages observed in the NFI data, covering a species diversity gradient nested within a climate gradient. We quantified functional diversity and the mean position of each species assemblage at equilibrium on two functional axis: (i) conservative *vs.* fast growing and (ii) low *vs.* high recruitment. We disturbed each species assemblage from equilibrium using species-specific storm disturbance mortality probabilities and quantified the assemblages' resistance (inverse of immediate basal area loss), recovery (slope of post-disturbance increase in basal area) and resilience (inverse of the cumulative deviation of basal area from the undisturbed state).

3. We found that on average, species-rich assemblages had higher recovery and resilience to storm disturbance, while functional diversity improved

35 resistance and recovery. When analyzing how this effect varied with climate,  
36 we found that diversity significantly increased resistance and resilience in  
37 the climatic margins only. Finally, we found that storm resilience was also  
38 driven by species mean position along both functional axes. In particular,  
39 the conservative-productive axis had an effect two to three times greater than  
40 diversity: forests dominated by conservative species were more resistant and  
41 resilient, but had lower recovery than species assemblages dominated by fast-  
42 growing species.

43

44 4. Taken together, these results show that climate and tree species com-  
45 position interact to control the ability of forests to resist and recover from  
46 a storm disturbance through both direct and indirect effects. As such, our  
47 findings should help to better anticipate climate change consequences for for-  
48 est ecosystems.

49

50 **Key-words:** forest dynamics, integral projection model, disturbance,  
51 storm, climate change

## 52 **2 Introduction**

53 In recent decades, natural disturbances such as fires, storms or insect out-  
54 breaks have been shown to increase in magnitude, severity and frequency  
55 (Allen et al., 2010; Senf et al., 2018; Taccoen et al., 2019; Yi et al., 2022;  
56 Patacca et al., 2022), resulting in increased tree mortality worldwide (Mc-  
57 Dowell et al., 2020) and loss of forest ecosystem services (Thom et al., 2016).  
58 In Europe, windstorms are reported to be the main disturbance agent both in  
59 terms of area (*i.e.* 2.5 million ha between 2002 and 2016 based on Senf et al.,  
60 2021) and in terms of timber volume affected (*i.e.* 40 million  $m^3$  per year be-  
61 tween 2000 and 2020 based on Patacca et al., 2022). Storm disturbances are  
62 characterized by important temporal variability, with a few years affected  
63 by large-scale storm events with continental-scale impacts (e.g., Lothar in  
64 1999). Although the relationship between climate change and storm dis-  
65 turbance regimes is less clear than for other disturbance types such as fire  
66 or bark beetle (Seneviratne et al., 2021), an increase in storm related tree  
67 mortality has been clearly identified in Europe over the last four decades  
68 (Senf et al., 2021; Patacca et al., 2022). In this context, the identification of  
69 factors that promote forest resilience to storm disturbances seems crucial to  
70 anticipate the impacts of global change on European forests.

71

72 The concept of resilience, introduced in ecology by Holling, 1973, encom-  
73 passes a wide range of definitions that are widely discussed in the literature  
74 (Mori, 2016; Nikinmaa et al., 2020; Yi et al., 2021; Albrich et al., 2022).  
75 However, the main definitions of resilience used in forest research (*e.g.*, eco-  
76 logical resilience, engineering resilience) generally converge on the idea that it

77 encompasses both the forest's ability to persist during the disturbance (here-  
78 after resistance) and its ability to 'bounce back' and return to an equilibrium  
79 (hereafter recovery) (Lloret et al., 2011; Nimmo et al., 2015; Capdevila et  
80 al., 2022). Resistance and recovery are rarely studied together due to the  
81 difficulty of tracking these metrics independently. However, resistance and  
82 recovery are driven by different demographic processes (*i.e.* survival for re-  
83 sistance, growth and recruitment for recovery) (Falk et al., 2022) and can  
84 therefore be expected to respond differently to environmental variation. De-  
85 composing resilience into resistance and recovery is thus important to better  
86 understand the mechanisms underlying the relationship between environmen-  
87 tal conditions and resilience.

88

89 Pre-disturbance tree species richness is one of the key drivers of resilience,  
90 affecting both resistance and recovery (Isbell et al., 2015; Schmitt et al.,  
91 2020). Recovery, which is strongly related to productivity (Falk et al., 2022),  
92 is expected to increase with species richness due to higher complementar-  
93 ity between species, which allows for more complete use of resources (Morin  
94 et al., 2011; Delalandre et al., 2022), and through the sampling effect - *i.e.*,  
95 fast-growing species are more likely to be present in diverse communities  
96 (Tilman, 2001; Loreau et al., 2001). Resistance is also known to increase  
97 with diversity in the case of biotic disturbances, as higher species richness  
98 tends to reduce resources for host-specific pests (Jactel et al., 2007), but the  
99 effect of species richness on resistance to storm disturbances remains largely  
100 unknown. Due to high interspecific differences in tree species resistance to  
101 storm disturbance (Canham et al., 2001; Trouvé et al., 2021; Barrere et al.,

102 2023), an overall positive effect of tree species richness on storm resistance  
103 could be expected through the sampling effect - *i.e.*, storm-resistant species  
104 being more likely to be present in diverse tree communities - but this hy-  
105 pothesis remains to be tested.

106

107 Functional diversity is increasingly seen as an alternative metric to species  
108 richness that better captures the effect of diversity on ecosystem functioning  
109 (Cadotte et al., 2011), but studies testing the effect of functional diversity  
110 on resilience remain surprisingly scarce but see Schmitt et al., 2020. In addi-  
111 tion to functional diversity, studies of herbaceous communities also suggest  
112 that community mean functional strategy (*i.e.*, the mean value of one or more  
113 traits weighted by species abundance, Muscarella et al., 2016) may have a key  
114 influence on their demography (Lepš et al., 1982; de Bello et al., 2021), but  
115 this has rarely been tested in the context of the resilience of tree communities.  
116 Consistently with the positive correlation between tree species productivity  
117 and mortality rates (Stephenson et al., 2011; Esquivel-Muelbert et al., 2020),  
118 the functional traits conferring resistance to storm disturbances also charac-  
119 terize conservative, slow-growing species - *i.e.*, high wood density, slow radial  
120 growth, low height to diameter ratio (Barrere et al., 2023). This suggests the  
121 existence of a functional trade-off between high storm resistance in forests  
122 dominated by slow growing species and fast recovery in forests dominated by  
123 fast-growing species (Nimmo et al., 2015). Beyond the resistance-recovery  
124 continuum, Ruger et al., 2018 also suggest the existence of an orthogonal de-  
125 mographic trade-off between high recruitment *vs* high survival and growth of  
126 adult trees. However, as resistance and recovery are rarely studied together,

127 it remains to be determined which of these strategies best promotes storm  
128 resilience and how diversity along these functional trade-offs affects resilience.

129

130 As intensification of disturbance regimes has been reported to affect all  
131 biomes (Yi et al., 2022), understanding the relationship between tree species  
132 composition and resilience on a global scale also requires consideration of  
133 the interactive effects of climate. First, climate can directly influence re-  
134 siliance metrics through physiological effects. For example, since recovery  
135 relies largely on the survival and establishment of seedlings and saplings  
136 (Falk et al., 2022), recovery should be optimal in more productive climates.  
137 Second, climate may also influence the relationship between diversity and  
138 resilience. The stress-gradient hypothesis theorises a shift from competi-  
139 tive interactions in productive environments to facilitation as environmental  
140 conditions become more severe, based on the idea that neighbors generally  
141 limit physical stress in harsh environments (Bertness et al., 1994). Build-  
142 ing on this hypothesis, studies suggest that the effect of diversity on forest  
143 productivity should peak in stressful environments (Toïgo et al., 2015; Pa-  
144 quette et al., 2011; Jucker et al., 2016). We might thus expect a greater  
145 effect of diversity on forest recovery to disturbance under stressful climatic  
146 conditions, but empirical evidence for this hypothesis is still scarce. Finally,  
147 climate may indirectly influence resilience and recovery by influencing the  
148 dominant functional strategy of tree communities. For example, hotter and  
149 drier climates have been shown to favour species with traits associated with  
150 storm resistance (*e.g.*, slow radial growth and high wood density, Barrere  
151 et al., 2023), whereas productive climates should theoretically favour faster



152 growing species.

153

154 This study aims to elucidate the relationship between pre-disturbance  
155 species composition and basal area resistance and recovery following storm  
156 disturbance across a climatic gradient spanning the Mediterranean, temper-  
157 ate and boreal biomes. We investigated (i) the overall effect of mean func-  
158 tional strategy (along two functional axes, growth *vs* survival and low *vs*  
159 high recruitment), species diversity and functional diversity on resistance,  
160 recovery and resilience, (ii) how this effect varied along a climatic gradient,  
161 and (iii) the relative importance of direct and indirect climate effects on re-  
162 siliance. To achieve this, we used a simulation approach and implemented  
163 species-specific storm disturbance mortality equations from the correlative  
164 study of Barrere et al., 2023 into a European-scale calibrated integral projec-  
165 tion model (IPM) (Kunstler et al., 2020; Guyennon et al., 2023). Simulation  
166 approaches are particularly suited to the study of forest resilience due to  
167 the long timescale of forest dynamics (Albrich et al., 2022). The key origi-  
168 nality of our modelling approach is to include species-specific sensitivity to  
169 disturbance and vital rates to model resistance and recovery independently,  
170 whereas most simulation studies on forest resilience apply a generic distur-  
171 bance without considering differences in resistance between species *e.g.*, see  
172 Schmitt et al., 2020; Guyennon et al., 2023.

## 173 **3 Material and methods**

### 174 **3.1 The integral projection model**

175 We used an integral projection model (IPM), that had already been cal-  
176 ibrated with National Forest Inventory (NFI) data. Here we present the  
177 main structure of the model, which is presented in Kunstler et al., 2020 and  
178 in Guyennon et al., 2023, without repeating in detail the calibration process.  
179 We present in detail all the new additions to the model.

180

#### 181 **3.1.1 Structure of the original IPM**

182 An IPM aims to describe how the distribution of a continuous trait (in this  
183 study, tree size as measured by diameter at breast height, hereafter dbh)  
184 for a population changes over time (Easterling et al., 2000). The main dif-  
185 ference with individual tree-based models is that IPMs integrate over the  
186 uncertainty in vital rates for their population forecast, and thus do not in-  
187 clude the demographic stochasticity that leads to variation between repli-  
188 cated simulations. More specifically, an IPM predicts the size distribution of  
189 a population  $n(z', t + 1)$  at time  $t + 1$  from its distribution  $n(z, t)$  at time  $t$   
190 using the following equation:

191

$$n(z', t + 1) = \int_L^U K(z', z)n(z, t)dz \quad (1)$$

192 L and U are the lower and upper bounds, respectively, of the values taken  
193 by the state variable  $z$  (*i.e.*, minimum and maximum tree dbh observed).

194  $K(z', z)$  is the projection kernel and is divided into subkernels as follows :

$$K(z', z) = s(z)G(z', z) + F(z', z) \quad (2)$$

195 Where  $s(z)$  is the survival function,  $G(z', z)$  is the growth kernel, which  
196 gives the probability that an individual of size  $z$  will reach size  $z'$ , and  $F(z', z)$   
197 is the fecundity kernel, which gives the size distribution of recruited trees at  
198 time  $t + 1$  based on the size distribution at time  $t$ .

199

### 200 **3.1.2 Model calibration**

201 *National Forest Inventory data* - The IPM was calibrated with data from the  
202 FunDivEUROPE platform (Baeten et al., 2013; Ratcliffe et al., 2017), which  
203 includes National Forest Inventories (NFI) from Spain, France, Germany,  
204 Sweden and Finland. Although protocols differ slightly between countries,  
205 all NFI plots were circular, with a sampling radius that varied according to  
206 tree dbh. All NFI plots were surveyed twice (survey interval of 9 years in av-  
207 erage, ranging between 5 and 20 years) and included measurements of species  
208 identity, diameter at breast height (dbh) and status (live, dead, harvested or  
209 ingrowing) for all trees with dbh greater than 10 cm. The protocol for each  
210 country is detailed in Supporting Information A.

211

212 *Climatic data* - The local climate of NFI plots was described using two  
213 annual climatic indices that represent well the European climatic gradient  
214 (overall ranging from hot-dry in the Mediterranean region to cold-wet in  
215 northern Scandinavia), and which are known to control tree growth, sur-

216 vival and recruitment in Europe (Kunstler et al., 2011): the annual sum  
217 of growing degree days above 5.5°C (sgdd) and the water availability index  
218 (wai), calculated as  $(P - PET)/PET$  - where P and PET are annual precipi-  
219 tation and potential evapotranspiration, respectively. sgdd is related to the  
220 mean annual temperature and the length of the growing season, and wai is  
221 negatively correlated to water stress. Daily temperature and P data were  
222 extracted from the spatially downscaled gridded climatic data of (Moreno  
223 et al., 2016). PET data were extracted from the gridded climatic data of the  
224 Climate Research Unit (CRU) (Harris et al., 2014). In each NFI plot, the  
225 value of these two indices was averaged over a period ranging from 1991 to  
226 2000. We chose this time period since it covers well the time period of the  
227 data used to calibrate the IPM model (see supporting information A) while  
228 being homogeneous across all countries.

229

230 *Demographic functions* - For each species included in the IPM, vital rates  
231 (*i.e.*, growth, survival and recruitment) were modeled with equations cali-  
232 brated with the NFI data. Full equations for survival, growth and recruit-  
233 ment are described in supporting information B. Growth and survival were  
234 modeled as a function of tree dbh, local climatic variables (sgdd and wai) and  
235 local competition, measured as the sum of basal area of all competitors. In  
236 addition of the survival function, a constant harvesting rate of 0.5% of tress  
237 of all size classes every five years (*i.e.*, average harvest rate in the calibration  
238 dataset) was also implemented to avoid predicting unrealistic life spans. Be-  
239 cause the processes of seed production, germination and seedling growth and  
240 survival were not recorded in the NFI data, the size distribution of recruits

241 was simply a function of fecundity (measured by the cumulative basal area  
242 of the species) and local competition (measured by the cumulative basal area  
243 of competitors, with a different effect for conspecific and heterospecific com-  
244 petition). To account for the time taken by each species to reach recruitment  
245 size (*i.e.*, 10cm dbh), we used tree-level age data (measured on a subset of  
246 trees in each NFI plot) to infer a species-specific mean age at 10cm, which  
247 was included as a delay in the IPM (Supporting Information C). This for-  
248 mulation is a simplification of the regeneration process which is frequently  
249 used in ecology due to the difficulty to model the complexity of regeneration  
250 dynamics (*e.g.*, see Lines et al., 2020).

251

252 *Uncertainty in vital rates* - To account for uncertainty in vital rates, dif-  
253 ferent model formulations were fitted 100 times using a sample of 70% of  
254 the available dataset for each species and each vital rate. The AIC of each  
255 model was computed on the remaining 30% and for each re-sampling itera-  
256 tion, the formulation of the growth and survival model resulting in the lowest  
257 AIC was selected. The goodness of fit of the growth, recruitment, and sur-  
258 vival models computed with a cross-validation on the remaining 30% of the  
259 dataset over all re-sampling iterations showed good agreement with the data  
260 (see Supporting Information B). To simplify the simulations, we averaged  
261 the parameters of the 100 best growth and survival models per species to  
262 keep one single model per species instead of 100 (*i.e.*, one per re-sampling  
263 iteration). This simplification of the model did not have a strong effect on  
264 the mean predictions of the model (Supporting Information D).

265

### 266 **3.1.3 Disturbances in the IPM**

267 We implemented in the model the possibility to apply storm disturbances of  
268 different intensity (ranging from 0 to 1) at any time of the IPM simulations.  
269 When a storm is applied in a given year, the survival function is replaced by  
270 the species-specific equations from Barrere et al., 2023, which quantify the  
271 annual mortality probability of a given tree in a stand affected by a storm  
272 as a function of its dbh, dominance status (log ratio of tree dbh and stand  
273 quadratic diameter), and type and intensity of the storm. In simulations,  
274 disturbances were applied over three years to account for possible delayed  
275 effects of the storm on mortality.

276

## 277 **3.2 Simulation experiment**

### 278 **3.2.1 Selection of observed tree species assemblages per climate**

279 To investigate the effect of species diversity, climate and their interactions  
280 on resilience, we ran simulations with different levels of climate and species  
281 diversity. While most simulation studies on the effect of tree diversity select  
282 random species assemblages from a species pool, we chose to restrict our  
283 simulations to species assemblages that are observed in the NFI data and  
284 that are consistent with the local climate. The goal is to simulate realistic  
285 species assemblages and to account for the fact that climate can also affect  
286 resilience through changes in tree species composition (Morin et al., 2018).  
287 To do this, we used the NFI dataset to select observed species assemblages  
288 at different levels of species richness and under different climatic conditions.

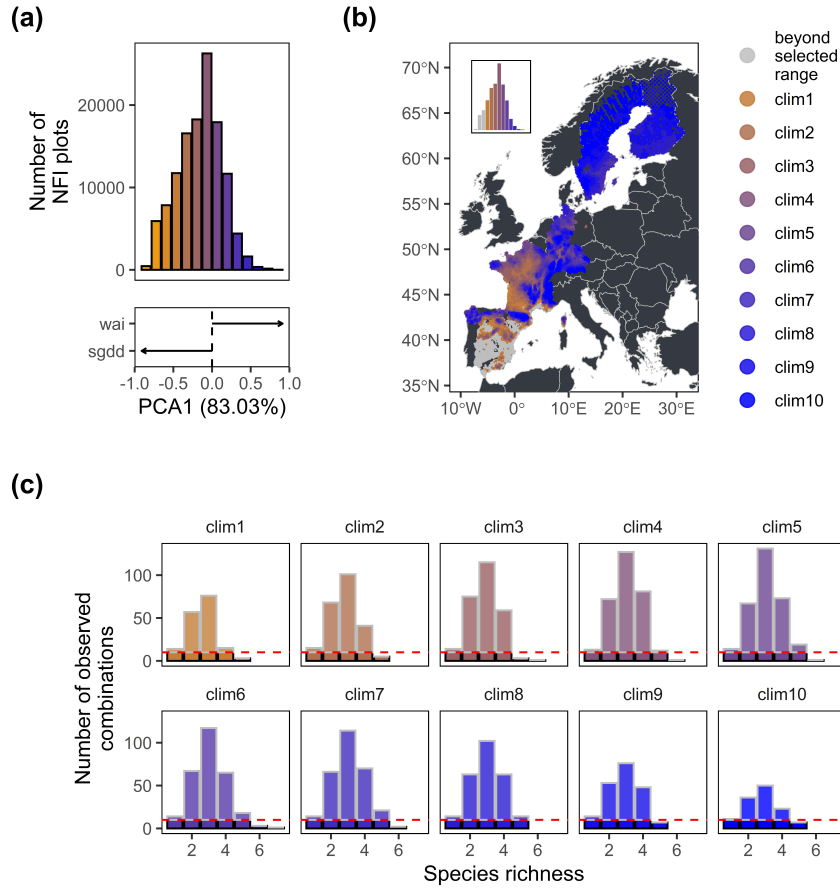


Figure 1: *Selection of tree species assemblages observed in NFI plots* - (a) Distribution of FunDiv NFI plots along the first axis of the sgdd-wai principal component analysis, (b) spatial distribution of the plots selected in the climatic gradient, and (c) number of tree species combinations observed per climate and species richness level. The red dotted line represents the maximum number of combinations selected for the simulations per richness and per climate.

290 *Climatic gradient* - Following Kunstler et al., 2020, we accounted for the  
291 strong correlation between sgdd and wai by characterising the NFI plots  
292 with their coordinates on the first axis of the pca of these two climate indices  
293 (83.6% of variance explained, Fig. 1.a). Low and high values along this axis  
294 characterise hot-dry and cold-wet climates respectively. As several species  
295 that were dominant at the hot and dry edge of our dataset were not included  
296 in the IPM, we chose to restrict our analysis to climates between the 20% and  
297 100% quantiles of NFI plot coordinates on the pca axis (Fig. 1). We grouped  
298 all NFI plots within this range into 10 subclimates based on quantiles of the  
299 climate axis, so that each climate group contained the same number of NFI  
300 plots (Fig. 1.b). When running simulations for a species assemblage from  
301 a given subclimate, we used the mean sgdd and wai of all NFI plots within  
302 that subclimate as the reference climate.

303

304 *Species diversity gradient* - We restricted the observed species assemblages  
305 to tree species that were both present in the IPM (see Guyennon et al., 2023  
306 and Kunstler et al., 2020 for the full species list), and for which there was an  
307 estimation of storm sensitivity in Barrere et al., 2023. In addition, we had  
308 to exclude from the simulations three species (*i.e.*, *Quercus ilex*, *Carpinus*  
309 *betulus* and *Salix caprea*) due to the high uncertainty in the demographic pa-  
310 rameters of their recruitment function leading to unrealistically high recruit-  
311 ment values, especially at high basal area (Guyennon et al., 2023). For *Q.*  
312 *ilex* and *C. betulus*, simulations even lead to exponential population growth  
313 and never reached an equilibrium. This high uncertainty is likely related to  
314 insufficient data for *Salix caprea* (only 0.2% of the basal area share in the



315 calibration dataset) and to the fact that *Q. ilex* and *C. betulus* are mostly  
316 managed in coppice, leading our statistical models to fail capturing the den-  
317 sity dependence limiting their high recruitment through resprouting. This  
318 resulted in a total of 14 species included in the simulations, listed in table 1.  
319 These 14 species represent altogether 78% of the basal share in the NFI plots  
320 (Fig. 1.b). To ensure comparable diversity gradients between subclimates,  
321 we selected the 10 most frequent combinations of these 14 tree species per  
322 observed level of species richness in each subclimate (Fig. 1.c). When less  
323 than 10 different species assemblages were observed for a given species rich-  
324 ness, we selected all observed species assemblages. This resulted in a total  
325 of 474 species assemblages being selected for the simulations (*i.e.*, 47.4 per  
326 subclimate in average).

Table 1: Mean dbh, share in basal area and climatic niche (cold margin, optimum, hot margin) within the NFI dataset and trait value of the 15 species included in the simulations

	mean dbh	share in	wai/sgdd			trait	value
	(mm)	basal area (%)	cold mar.	optimum	hot mar.	PC1	PC2
<i>Abies alba</i>	250	3.9	1.15/575	0.45/1824	-0.01/2629	1.88	0.88
<i>Alnus glutinosa</i>	188	0.7	0.56/1482	0.09/2301	-0.34/3069	1.07	-1.32
<i>Fagus sylvatica</i>	217	10.6	0.87/817	0.18/2044	-0.19/2688	-1.59	1.28
<i>Fraxinus excelsior</i>	200	1.8	0.62/1348	0.05/2347	-0.32/2999	0.01	0.58
<i>Picea abies</i>	204	22.7	1/468	0.45/1445	0.03/2185	1.46	1.45
<i>Pinus halepensis</i>	174	2.3	-0.37/2844	-0.61/3274	-0.92/3813	-1.11	-0.09
<i>Pinus nigra</i>	179	2.8	-0.05/1756	-0.45/2470	-0.69/2886	-0.31	-1.26
<i>Pinus pinaster</i>	210	5.7	0.23/1888	-0.35/2911	-0.74/3613	0.95	0.39
<i>Pinus pinea</i>	208	0.8	-0.29/2973	-0.51/3351	-0.93/4109	-1.18	-0.23
<i>Pinus sylvestris</i>	200	14.9	0.53/874	0.05/1717	-0.45/2601	0.18	-0.75
<i>Pinus uncinata</i>	199	0.6	0.67/452	0.25/1195	-0.07/1771	-1.69	-1.45
<i>Populus tremula</i>	185	0.4	0.58/1185	-0.03/2275	-0.35/2825	2.88	-0.75
<i>Quercus petraea</i>	230	5.3	0.42/1602	-0.01/2371	-0.31/2898	-1.33	0.54
<i>Quercus robur</i>	249	5.5	0.43/1830	0/2582	-0.29/3092	-1.24	0.73

327 **3.2.2 Equilibrium and species composition metrics**

328 *Equilibrium state in IPM* - For each species assemblage, we ran simulations  
 329 from a random initial size distribution until variations in size distribution  
 330 over time became negligible - *i.e.* until the amplitude of change in total  
 331 stand basal area remained below  $0.5 \text{ m}^2.\text{ha}^{-1}$ . This allowed us to identify a  
 332 single equilibrium state per species assemblage-climate combination, which  
 333 we defined as the pre-disturbance state. Of the 465 species assemblages se-  
 334 lected, 37 did not reach equilibrium - *i.e.*, the amplitude of change in basal  
 335 area over time remained greater than  $0.5 \text{ m}^2.\text{ha}^{-1}$  after 50000 years of sim-  
 336 ulation from a random size distribution. These species assemblages were  
 337 therefore excluded from the dataset. This resulted in a total of 428 simu-  
 338 lations that were eventually included in the statistical models. For each of  
 339 the 428 species assemblages, we calculated species composition metrics (*i.e.*,  
 340 species diversity, functional diversity and mean functional strategy) at the  
 341 pre-disturbance equilibrium state.

342

343 *Species composition metrics* - We characterised tree species diversity in a  
 344 species assemblage  $i$  using the Shannon index ( $H_i$ ) to account for interspe-  
 345 cific differences in abundance (measured for a tree species  $j$  as its basal area  
 346 at equilibrium  $BA_{eq_{ij}}$ ) at equilibrium:

347

$$H_i = \sum_j^{N_i} p_{ij} * \log(p_{ij}) \quad \text{with} \quad p_{ij} = \frac{BA_{eq_{ij}}}{\sum_j^{N_i} BA_{eq_{ij}}} \quad (3)$$

348 Where  $N_i$  in the number of species present in species assemblage  $i$ .

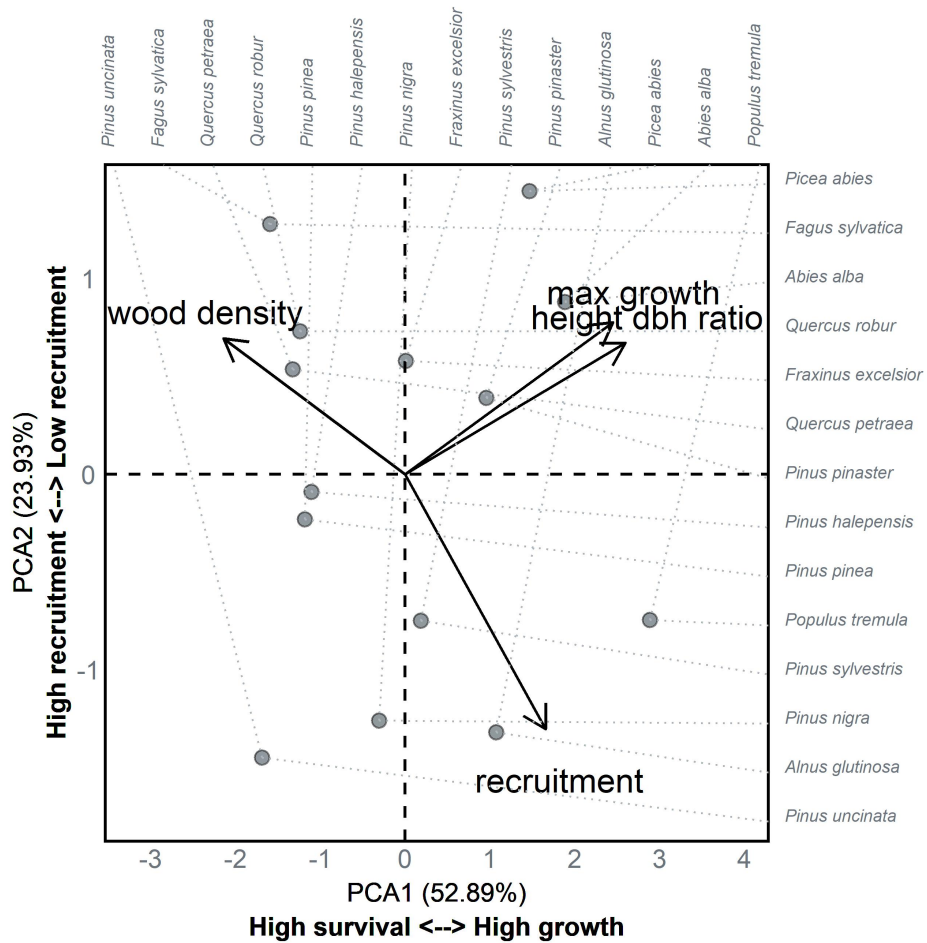


Figure 2: Position of each species included in the IPM along the two first axes of the principal component analysis of the functional traits.

350 To calculate functional diversity and the mean functional strategy, we  
 351 chose to focus on two functional axes analogous to the two main demo-  
 352 graphic dimensions structuring tree communities in Ruger et al., 2018: (1)

353 the growth-survival trade-off and (2) the recruitment axis. To quantify the  
354 growth-survival axis, we used three functional traits (*i.e.*, wood density,  
355 height/dbh ratio and maximum radial growth) that were shown to corre-  
356 late well with the sensitivity of tree species to storm disturbance (Barrere  
357 et al., 2023) and that are available for most of the species studied. These  
358 three traits were available for 22 of the 27 species present in the IMP (in-  
359 cluding the 14 selected for the simulations) from the wood density database  
360 (Chave et al., 2009) and from Barrere et al., 2023. All traits were calculated  
361 for adult trees (defined for traits calculated from NFI data as trees with a  
362 dbh higher than 10cm). We quantified the recruitment axis with a single  
363 trait: the recruitment of each species at their climatic optimum, and for the  
364 average conditions of intra and inter-specific competition across the dataset  
365 (17 and 6  $m^2.ha^{-1}$  of basal area, respectively). This trait, hereafter referred  
366 to as recruitment rate, was calculated using the recruitment function of the  
367 IPM described in supporting information B. We chose to use this trait cal-  
368 culated from demographic parameters of our model due to the difficulty to  
369 find trait that reflects the whole process of recruitment (*i.e.*, both fecundity  
370 and regeneration dynamics). The first axis of the principal component anal-  
371 ysis (PCA1) with these four traits contrasted fast-growing species (*i.e.*, high  
372 maximum growth and height/dbh ratio) with slow-growing resistant species  
373 (*i.e.*, high wood density) (Fig. 2). The second axis of the principal compo-  
374 nent analysis (PCA2) contrasted species with high and low recruitment rate  
375 (Fig. 2). In a species assemblage  $i$  with  $N_i$  species, we calculated the mean  
376 functional strategy along each of the two functional axes at equilibrium using  
377 community weighted mean ( $CWM1_i$  and  $CWM2_i$ ) - *i.e.*, the mean of species

378 coordinates along PCA1 and PCA2 respectively, weighted by their basal area  
 379 at equilibrium ( $BA_{eq}$ ). Functional diversity at equilibrium (FD) was calcu-  
 380 lated with the functional dispersion index (Laliberté et al., 2010), which is  
 381 the abundance-weighted mean distance  $z_j$  of each species  $j$  to the centroid  
 382 of all species of the community in the multivariate trait space formed by the  
 383 two functional axes:

$$\begin{cases} CWM1_i = \frac{\sum_j^{N_i} BA_{eqij} * PCA1_j}{\sum_j^{N_i} BA_{eqij}} \\ CWM2_i = \frac{\sum_j^{N_i} BA_{eqij} * PCA2_j}{\sum_j^{N_i} BA_{eqij}} \\ FD_i = \frac{\sum_j^{N_i} BA_{eqij} * z_j}{\sum_j^{N_i} BA_{eqij}} \end{cases} \quad (4)$$

### 384 3.2.3 Disturbances and resilience metrics

385 *Simulation of disturbance* - For each species assemblage, we applied a sin-  
 386 gle disturbance event from the equilibrium state and simulated the post-  
 387 disturbance trajectories over 3000 years. We applied the same disturbance  
 388 event to all species assemblages - *i.e.*, a storm disturbance of intensity 0.5,  
 389 which is the 90% quantile of the storm disturbance intensity distribution es-  
 390 timated across Europe in Barrere et al., 2023. As an illustration, for spruce  
 391 (*Picea abies*), fir (*Abies alba*) and pine (*Pinus sylvestris*) trees of 250 mm  
 392 dbh, such a disturbance (*i.e.* storm of intensity 0.5) corresponds to a proba-  
 393 bility of mortality of about 30%, 20% and 10%, respectively (see Supporting  
 394 Information E for example changes in basal area and species composition of  
 395 tree assemblages during post-disturbance simulations).

396

397 *Calculation of forest response to disturbance* - To quantify forest response

398 to disturbance in basal area, we calculated three different metrics: resistance,  
399 recovery and resilience. We calculated resistance as the ratio of the stand  
400 basal area immediately after the disturbance ( $BA_{dist}$ ) vs before, at equilib-  
401 rium ( $BA_{eq}$ ), as in many studies *e.g.*, see Lloret et al., 2011; Enright et al.,  
402 2014; Nimmo et al., 2015. As in João et al., 2018, we quantify recovery as  
403 the slope of the short-term (*i.e.*, 20 years) post-disturbance increase in basal  
404 area. Finally, we quantify resilience as the inverse of the integration over  
405 time of the difference in basal area from the undisturbed state, as in Schmitt  
406 et al., 2020, so that resilience correlates positively with both the forest’s abil-  
407 ity to resist and to recover from a disturbance (Fig. 3).

408 Unlike other studies that explored resilience not only in term of forest struc-  
409 ture but also in species composition (*e.g.*, Sánchez-Pinillos et al., 2019), we  
410 focused in this study on forest response in term of total basal area only.  
411 Indeed, in the IPM model, forests that recovered the pre-disturbance state  
412 in term of basal area systematically returned to the same species composi-  
413 tion, so that metrics of change in species composition are highly correlated  
414 to metrics of change in basal area (see supporting Information F).

### 415 **3.3 Data analysis**

416 *Effect of species composition on resistance, recovery and resilience* - We fit-  
417 ted three simple linear models, one for each forest response metric (*i.e.*,  
418 resistance, recovery and resilience), each with the four species composition  
419 metrics (H, FD, CWM1 and CWM2) as explanatory variables.

420

421 *Consistency of species composition effect across climates* - To test whether

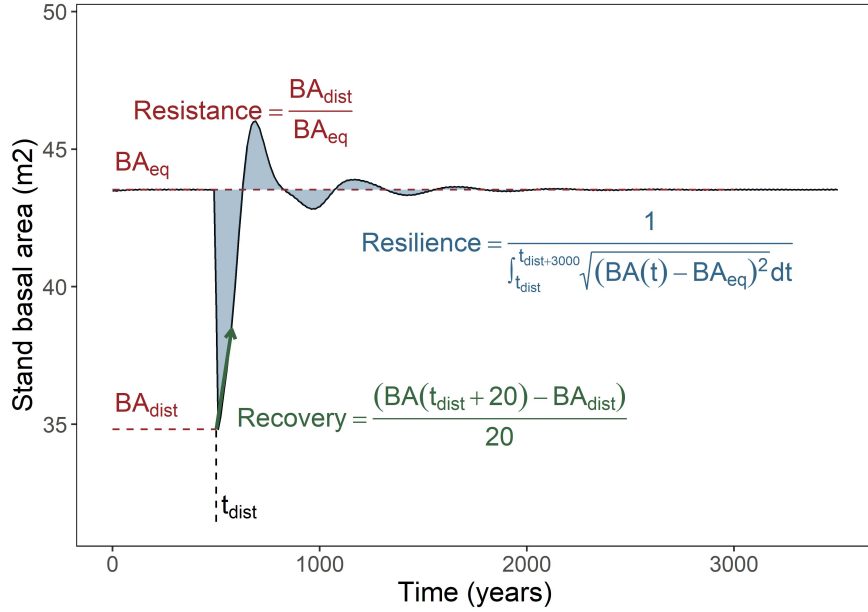


Figure 3: Schematic representation of the metric representing resistance, recovery and resilience to storm in our study.

422 the effect of species composition on forest response to disturbance is influ-  
 423 enced by climate, we fitted a model for each forest response metric with  
 424 species composition metrics, climate (*i.e.*, first axis of the wai-sgdd pca, Fig.  
 425 1.a) and a quadratic effect of climate as explanatory variables to account for  
 426 potential non-linear effects. We fitted models including all possible combina-  
 427 tions of interactions between species composition metrics and climate, and  
 428 selected the most parsimonious one based on the AIC criterion.

429

430 *Direct and indirect effects of climate on forest response* - To disentangle  
 431 the direct effect of climate on resistance, recovery and resilience from indi-  
 432 rect effects through climate-induced changes in tree species composition, we



433 used structural equation modelling (SEM). SEM allows multiple models to be  
434 combined into a single causal network, where variables can be both response  
435 and explanatory variables. We constructed the SEM network based on a pri-  
436 ori knowledge of the relationships between variables. We included a total of  
437 7 sub-models, described in Supporting information G, with the four species  
438 composition metrics and the three forest response metrics as response vari-  
439 ables. We used a peacewise SEM (Lefcheck, 2016), which, unlike traditional  
440 SEM, allows the inclusion of models with non-normal error distributions. In  
441 our SEM analysis, all models had a normal error distribution, except for the  
442 two sub-models with FD and H as response variables, for which we used  
443 a generalised linear model with a Tweedie error distribution to account for  
444 the continuous zero-inflated distribution of these variables (Lecomte et al.,  
445 2013). For each sub-models, we reported the direct, indirect and total effect  
446 of each explanatory variable using the semEff R package (Murphy, 2023). We  
447 estimated 95% confidence intervals for total effects using 1000 bootstrap runs.

448

449 Explanatory variables were centred and scaled in all statistical models.  
450 We log-transformed recovery and resilience and logit-transformed resistance  
451 to meet normality assumptions. All statistical analyses were performed using  
452 R.4.1.2 (RCoreTeam, 2019) in Rstudio version 2021.9.1.372 (RStudioTeam,  
453 2021). The IPM model is implemented in the R package matreex, ver-  
454 sion 0.3 (Jaunatre et al., 2023) available at [https://github.com/gowachin/](https://github.com/gowachin/matreex)  
455 **matreex**. We used the *peacewiseSEM* package (version 2.1) to fit the SEM  
456 analysis (Lefcheck, 2016).

457 **4 Results**

458 **4.1 Direct effect of species composition on resilience**

459 Linear models testing the effects of species composition metrics on resistance,  
460 recovery and resilience reveal a predominant role of the species functional  
461 strategy followed by a smaller positive effect of species diversity and func-  
462 tional diversity.

463

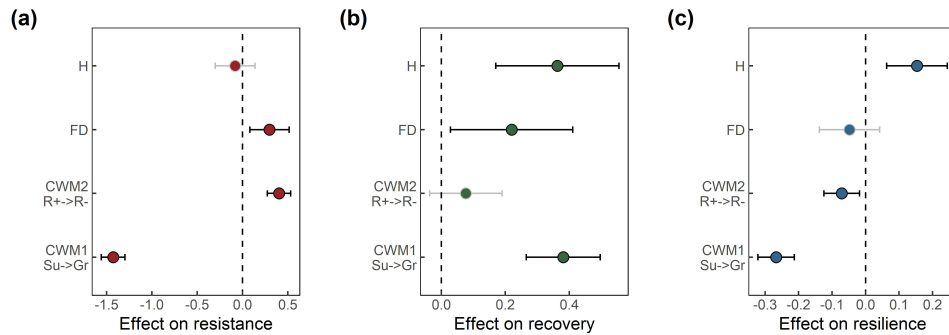


Figure 4: Effect of species composition metrics - Shannon index (H), functional diversity (FD) and mean functional strategy along the growth-survival (CWM1) and recruitment (CWM2) axes - on resistance, recovery and resilience to storm.

464 *Functional strategy effect* - Mean functional strategy on the growth-survival  
465 (CWM1) and recruitment (CWM2) axes had a strong significant effect on  
466 the three forest response metrics. In particular, the effect of CWM1 was  
467 of an order of magnitude higher (on resistance and resilience) or equal (on  
468 recovery) to the effect of diversity (Fig. 4). Species assemblages dominated

469 by species with high wood density, slow radial growth and low height to dbh  
470 ratio were more resistant and resilient, but had lower recovery. The effect of  
471 CWM2 was relatively small in magnitude but significant for both resistance  
472 and resilience: species assemblages dominated by species with high recruit-  
473 ment rate had low resistance but high resilience (Fig. 4).

474

475 *Diversity effect* - Species diversity (H) had a significant positive effect on  
476 recovery and resilience and functional diversity (FD) had a significant posi-  
477 tive effect on resistance and recovery (Fig. 4).

478

479 Detailed statistics of the three models, the analysis of the residuals and  
480 the relationship between predicted and observed values are provided in Sup-  
481 porting Information H.

## 482 **4.2 Consistency of the species composition effect across** 483 **climate**

484 Our linear models testing interactive effects with climate showed that the  
485 effect of species composition on response to disturbance was highly variable  
486 across climates, particularly for resistance.

487

488 *Resistance* - The effects of the four species composition metrics (*i.e.*,  
489 CWM1, CWM2, H and FD) on resistance all interacted significantly with  
490 climate. The positive effect of functional diversity on resistance was only  
491 significant at the hot and dry edge while the positive effect of species di-  
492 versity was only significant at the cold and wet edge. Species assemblages

493 dominated by slow-growing species were more resistant regardless of climate,  
 494 but this effect tended to be higher in hotter and drier climates. Finally, the  
 495 higher resistance of forests dominated by species with low recruitment rate  
 496 peaked in intermediate climates (Fig. 5).

497

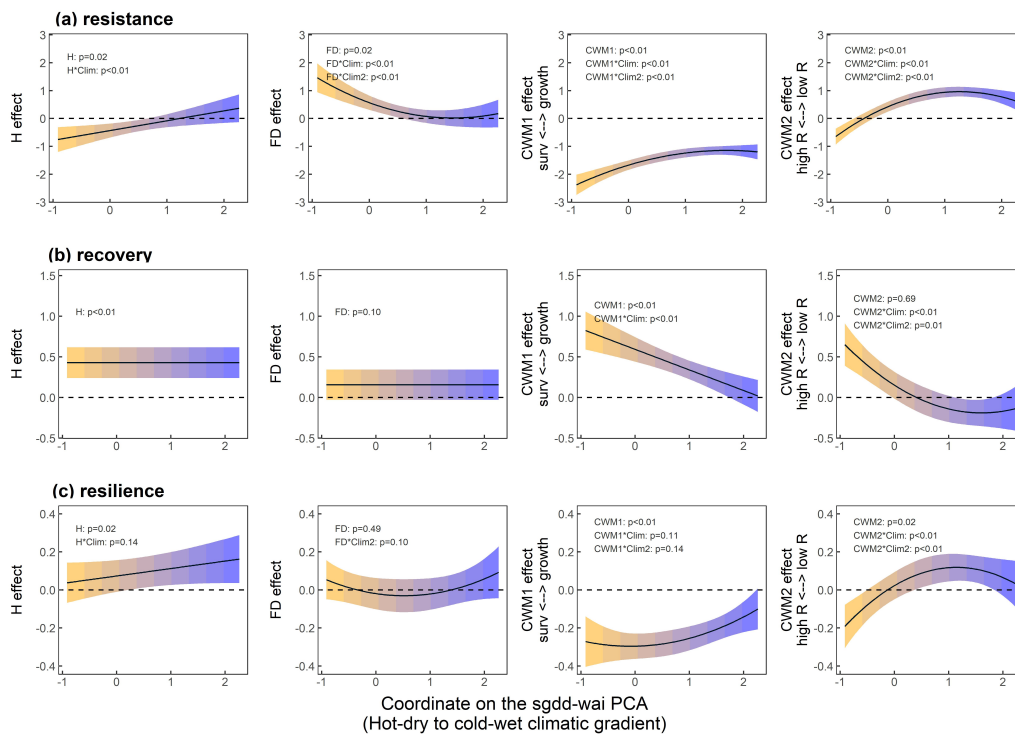


Figure 5: Effect of species composition metrics - Shannon index (R), functional diversity (FD) and mean functional strategy (CWM1 and CWM2) - on resistance, recovery and resilience to storm along the climatic gradient described in fig. 1

498 *Recovery* - The effect of mean functional strategy on recovery significantly  
 499 interacted with the climate quadratic term. The positive effect of CWM1 on

500 recovery (*i.e.*, communities dominated by species with low wood density and  
501 fast radial growth recover faster) peaked in hot and dry climates (Fig. 5).  
502 The effect of CWM2 on recovery was negative (*i.e.*, communities dominated  
503 by species with high recruitment rate recover faster) at the cold and wet  
504 edge, and positive at the hot and dry climatic edge (Fig. 5). Interactions  
505 between the effects of diversity (H and FD) and climate on recovery were not  
506 significant. Including climate in the recovery model therefore did not change  
507 the effect of these two variables - *i.e.*, significantly positive (Fig. 5).

508

509 *Resilience* - The effect of mean functional strategy on resilience interacted  
510 significantly with both climate and its quadratic term. The negative effect of  
511 CWM1 on resilience (*i.e.*, communities dominated by species with high wood  
512 density and slow radial growth are more resilient) peaked in hot and dry cli-  
513 mates (Fig. 5). Assemblages dominated by species with high recruitment  
514 rate were significantly more resilient at the hot and dry edge, and signifi-  
515 cantly less resilient at intermediate climates. The effect of species diversity  
516 (H) on resilience was significant in cold and wet climates, but not in hot and  
517 dry climates. Finally, the non-significant effect of functional diversity (FD)  
518 on resilience was not affected by climate (Fig. 5).

519

520 Detailed statistics of the three models and the relationship between pre-  
521 dicted and observed values are provided in Supporting Information I.

522

523 **4.3 Direct and indirect effects of climate on forest re-**  
524 **sponse to disturbance**

525 The structural equation model (SEM) showed that overall resilience was  
526 higher in hotter and drier climates. This trend was primarily driven by di-  
527 rect effects, while indirect effects through climate-induced changes in species  
528 composition were of secondary importance.

529

Table 2: Direct, indirect and total effect of each explanatory variable on each response variable in the structural equation model. Total effect is the sum of both direct and indirect effects. \* indicates significance.

Response variable	Explanatory variable	Direct effect Est. (95% CI)	Indirect effect Est. (95% CI)	Total effect Est. (95% CI)
H	climate	0.003 (-0.007-0.012)		0.003 (-0.007-0.012)
FD	climate	0.01 (0.002-0.017)*	0 (-0.001-0.001)	0.01 (0.002-0.017)*
FD	H	0.113 (0.106-0.119)*		0.113 (0.106-0.119)*
CWM1	climate	-0.012 (-0.115-0.09)		-0.012 (-0.115-0.09)
CWM2	climate	0.334 (0.222-0.435)*		0.334 (0.222-0.435)*
resistance	climate	-0.067 (-0.131-0.004)*	0.068 (0.001-0.136)*	0.001 (-0.078-0.084)
resistance	CWM1	-0.597 (-0.646-0.549)*		-0.597 (-0.646-0.549)*
resistance	CWM2	0.184 (0.094-0.266)*		0.184 (0.094-0.266)*
resistance	FD	0.082 (0.042-0.122)*		0.082 (0.042-0.122)*
resistance	H	-0.028 (-0.07-0.018)	0.009 (0.005-0.014)*	-0.018 (-0.058-0.025)
recovery	climate	0.035 (-0.069-0.137)	0.013 (-0.034-0.066)	0.048 (-0.042-0.133)
recovery	CWM1	0.266 (0.122-0.403)*		0.266 (0.122-0.403)*
recovery	CWM2	0.038 (-0.068-0.146)		0.038 (-0.068-0.146)
recovery	FD	0.086 (0.023-0.148)*		0.086 (0.023-0.148)*
recovery	H	0.156 (0.095-0.218)*	0.01 (0.003-0.017)*	0.166 (0.109-0.222)*
resilience	climate	-0.313 (-0.377-0.248)*	-0.031 (-0.07-0.01)	-0.344 (-0.403-0.278)*
resilience	CWM1	0.04 (-0.045-0.123)	-0.248 (-0.287-0.206)*	-0.208 (-0.281-0.133)*
resilience	CWM2	-0.059 (-0.114-0.001)*	0.046 (-0.012-0.098)	-0.012 (-0.084-0.055)
resilience	FD	-0.025 (-0.08-0.028)	0.003 (-0.024-0.031)	-0.022 (-0.08-0.035)
resilience	H	0.158 (0.094-0.22)*	-0.05 (-0.078-0.021)*	0.108 (0.051-0.164)*
resilience	recovery	-0.253 (-0.358-0.119)*		-0.253 (-0.358-0.119)*
resilience	resistance	0.308 (0.237-0.383)*		0.308 (0.237-0.383)*

530 The SEM we fitted (AIC = 267) resulted in a majority of significant re-  
531 lationships between variables and relatively high  $R^2$  in the submodels of the

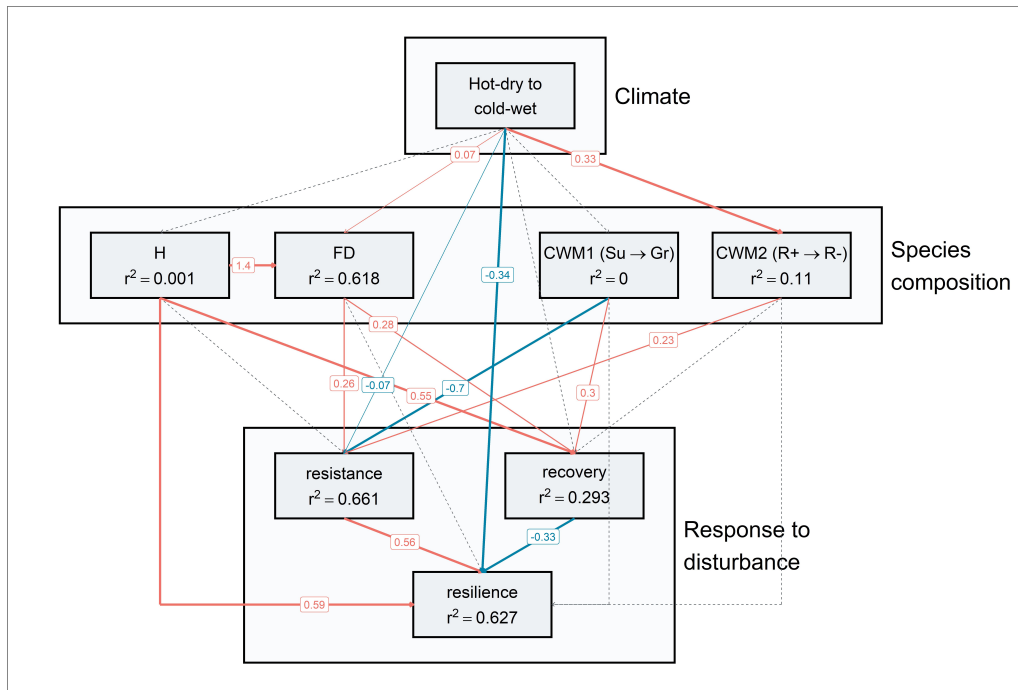


Figure 6: Structural equation model predicting the direct and indirect (via changes in species composition) effects of climate on resistance, recovery and resilience to storm. Red solid lines, blue solid lines and grey dotted lines respectively indicates significant positive, significant negative and non significant effects.

532 SEM (i.e.  $R^2$  higher than 60% in three out of the seven submodels) (Fig. 6),  
 533 indicating a good quality of fit (Hertzog, 2019). Although Shipley's direct  
 534 separation test suggests that some relationships between variables may be  
 535 missing in our SEM (Fisher's  $C = 215$ ,  $df = 12$ ,  $p < 0.01$ ), a more complete  
 536 SEM including additional relationships to satisfy Shipley's test yielded the  
 537 same magnitude of the effects we tested (see Supporting Information J).

538

539 The structural equation model shows that forests from colder and wetter  
540 climate are more functionally diverse and are dominated by species with low  
541 recruitment rate (Fig. 6). These climate-induced changes in tree species  
542 composition significantly increases resistance indirectly but have no signifi-  
543 cant indirect effect on recovery nor on resilience (table 2). This indirect effect  
544 of climate on resistance is offset by a significant direct effect in the opposite  
545 direction (*i.e.*, higher resistance in hot and dry climate, Fig. 6), resulting in  
546 an overall non-significant effect of climate on resistance (table 2). Finally,  
547 our SEM analysis shows that forests are overall more resilient in hotter and  
548 drier climates, but that this is not related to changes in tree species compo-  
549 sition (table 2).

550

## 551 **5 Discussion**

### 552 **5.1 Tree species composition drives resistance, recovery and resilience to storm disturbance**

553

554 *The key effect of mean functional strategy* - Our simulation experiment showed  
555 that in Europe, forests dominated by conservative species (*i.e.*, high wood  
556 density, slow radial growth) had lower recovery but higher resistance and re-  
557 siliance than forests dominated by fast-growing species. This suggests that,  
558 under the conditions of our model, a forest's ability to resist and survive storm  
559 disturbance contributes more to its resilience than its rate of recovery. This  
560 result is broadly consistent with previous field studies that reported greater



561 resilience in tropical tree communities dominated by conservative species  
562 (Hérault et al., 2018) or boreal tree communities dominated by broadleaf  
563 species (White et al., 2023), despite their slower growth rates. More sur-  
564 prisingly, we observed that the effect of the mean functional strategy of the  
565 community on resilience was much stronger in magnitude than the effects  
566 of species diversity and functional diversity. The idea that the traits of the  
567 dominant species in a community contribute more to resilience and recovery  
568 than diversity has been documented in studies of herbaceous communities  
569 (Lepš et al., 1982; Grime, 1998; de Bello et al., 2021), but our study is the  
570 first, to our knowledge, to show that this trend can also apply to forest tree  
571 communities. However, it is important to note that in the dataset used to  
572 calibrate the storm mortality equations and which guided the set of traits  
573 chosen for this study, information on the exact mechanisms causing storm  
574 mortality (e.g., windthrow, mechanical failure of the bole in the presence of  
575 fungal saprotrophs, etc.) was not available (Barrere et al., 2023). Thus, the  
576 traits chosen as proxies for storm sensitivity were relatively generic (radial  
577 growth, wood density). Better knowledge of the mechanisms at play, to-  
578 gether with a set of more adapted traits, might have resulted in a stronger  
579 effect of functional diversity. Finally, we showed that the mean position of  
580 tree species along the recruitment functional axis also contributed (although  
581 to a lower extent than the growth-survival trade-off) to explain forest demo-  
582 graphic response to storm disturbance. This is in agreement with the study  
583 of Rüger et al., 2018 in tropical context who showed that tree species demog-  
584 raphy is not only structured by the growth-survival trade-off but also by an  
585 orthogonal fecundity axis. Overall, our results argue for a more systematic

586 use of the community mean functional strategy in studies of the relationship  
587 between tree species composition and forest dynamics.

588

589 *Diverse forests are more resilient to storm* - One of the key findings from  
590 our simulations is also that diversity (*i.e.* species diversity and/or functional  
591 diversity) improves the ability of forests to both resist and recover from a  
592 storm disturbance. While the positive relationship between forest produc-  
593 tivity and biodiversity has been extensively studied in the literature (Morin  
594 et al., 2011; Jucker et al., 2016; Ammer, 2019), only a few studies have in-  
595 vestigated the effect of diversity on forest response to disturbance, and these  
596 have focused either on insect attack (Jactel et al., 2007; Jactel et al., 2017)  
597 or on a generic disturbance (Schmitt et al., 2020), but never on storm distur-  
598 bance. Considering resilience as the combination of resistance and recovery  
599 (Holling, 1973; Albrich et al., 2020), we show that the higher resilience of  
600 diverse forests is due to a positive effect of diversity on both resistance and  
601 recovery. Unlike most simulation studies of diversity effects, which use ran-  
602 dom species combinations to cover a broad diversity gradient (Morin et al.,  
603 2011; Schmitt et al., 2020), we chose to restrict our simulations to observed  
604 species assemblages, despite the low diversity gradient observed in European  
605 forests (*i.e.*, a maximum of 6 species in our simulations). This approach al-  
606 lowed us to show that a diversity effect on the resilience to storm disturbances  
607 is already noticeable for the short diversity gradients observed in European  
608 forests.

609

## 610 **5.2 Climate mediates the effect of species composition** 611 **on forest response to disturbance to storm**

612 *The diversity - recovery relationship is not affected by climate* - In line with  
613 the stress gradient hypothesis (Bertness et al., 1994), several field studies have  
614 shown that the effect of diversity on forest productivity peaks in harsher en-  
615 vironments with lower productivity and resource availability (Paquette et al.,  
616 2011; Toïgo et al., 2015; Jucker et al., 2016; Ratcliffe et al., 2017; Jactel et  
617 al., 2018). Due to the strong relationship between recovery and productivity  
618 (Falk et al., 2022), we might have expected this higher productivity under  
619 extreme conditions to translate into higher post-storm recovery. However,  
620 our simulations showed that the effect of diversity on recovery was constant  
621 across the European climatic gradient. The main explanation put forward  
622 to explain the stronger relationship between diversity and productivity un-  
623 der stressful conditions is that competition between species is reduced due  
624 to low productivity, leaving more room for facilitative interactions (Ammer,  
625 2019). Our finding may arise from the weaker competitive interactions un-  
626 der post-storm conditions: as recovery occurs at low stand densities following  
627 disturbance, biodiversity effects that promote productivity through reduced  
628 competition are less likely to occur.

629  
630 *The effect of species composition on resistance is highly sensitive to cli-*  
631 *mate* - While many studies have examined the effect of climate on the  
632 diversity-productivity relationship (Toïgo et al., 2015; Jucker et al., 2016;  
633 Jactel et al., 2018), its effect on the relationship between diversity and resis-  
634 tance to disturbance has been much less investigated. In this study, we found

635 that the positive effect of diversity on resistance to storm disturbance peaked  
636 at the two extremes of the climatic gradient. Due to the positive correlation  
637 between resistance and resilience (Fig. 6), this also resulted in a similar  
638 but weaker trend for the diversity-resilience relationship. In a previous field  
639 study, Guyot et al., 2016 found that the positive effect of diversity on re-  
640 sistance to biotic disturbance was constant across a European-scale climatic  
641 gradient. The difference between our results and those of Guyot et al., 2016 is  
642 likely due to differences in the mechanisms underlying the diversity-resistance  
643 relationship between biotic and storm disturbances. In their review, Jactel  
644 et al., 2017 suggest that for biotic damage, the resistance-diversity relation  
645 is mainly driven by association effects (*e.g.*, fewer hosts are available in di-  
646 verse stands for specialist pests), whereas the windstorm resistance-diversity  
647 relation is mainly driven by the sampling effect (*e.g.*, diverse species assem-  
648 blages are more likely to host storm-resistant species). The contribution of  
649 the sampling effect to the diversity-resistance relationship should be partic-  
650 ularly strong under the conditions of our model, as disturbance mortality  
651 depends solely on forest structure and species sensitivity. This effect is ex-  
652 pected to be particularly strong in harsher environments, where the propor-  
653 tion of slow-growing, resistant species is higher than in more growth-optimal  
654 climates, where most species tend to optimise productivity, leading to more  
655 functional redundancy (Wu et al., 2015; Barrere et al., 2023). Overall, our  
656 results support the idea that the relationship between diversity (*i.e.*, both  
657 functional diversity and species diversity) and ecosystem functioning can be  
658 highly variable depending on environmental variables such as climate (Rat-  
659 cliffe et al., 2017).

### 661 **5.3 Resilience is higher in hot and dry climates**

662 Our analyses show that, overall, forests tend to be more resilient in hot and  
663 dry climates. In addition to influencing the effect of diversity on resilience,  
664 climate has been reported to directly influence productivity through physi-  
665 ological effects (Ammer, 2019) and to alter species composition, which may  
666 indirectly influence both productivity (Morin et al., 2018) or resistance to  
667 disturbance (Rogers et al., 2017; Barrere et al., 2023). However, the con-  
668 tribution of indirect climate effects on storm resilience via changes in tree  
669 species composition has rarely been investigated. Previous studies focusing  
670 on productivity have found that climate has mainly indirect effects through  
671 changes in tree species composition (Morin et al., 2018; Delalandre et al.,  
672 2022). Our structural equation modelling (SEM) approach suggests the ex-  
673 istence of indirect climate effects on resistance through changes in species  
674 composition (*i.e.*, via FD and CWM2), with forests from cold and wet cli-  
675 mates being more resistant to storm due to a higher functional diversity and  
676 a lower proportion of species with high recruitment rate (*i.e.*, high CW2).  
677 However, we found that the indirect effects of climate on resilience were  
678 not significant, thereby suggesting that the higher resilience of forests from  
679 hot and dry climates is not related to changes in tree species composition.  
680 Given the hypotheses of our model, part of this climate effect on resilience  
681 unexplained by tree species composition could be related to climate-induced  
682 changes in forest structure at equilibrium which can further affect resilience  
683 (Cooper-Ellis et al., 1999). High temperatures and reduced water availability

684 have been shown to reduce average tree size (Astigarraga et al., 2020). This  
685 was also observed in our analyses, along with higher tree density and lower  
686 disturbance-induced changes in tree size distribution in hot and dry climates  
687 (Supporting information K). Taken together, our results highlight the fact  
688 that climate also contributes to shaping forest resilience to disturbance, and  
689 that the interactions between climate, tree species composition and resilience  
690 need to be considered when predicting forest dynamics under climate change.  
691

## 692 **5.4 Advantages and limitations of the modelling ap-** 693 **proach**

694 *Disentangling resistance from recovery to better understand the drivers of*  
695 *resilience* - One key originality of our study was to analyse resistance and  
696 recovery together. Indeed, due to the difficulty of capturing species-specific  
697 sensitivity to disturbance, studies simulating forest resilience tend to focus on  
698 recovery (Schmitt et al., 2020; Guyennon et al., 2023) without considering  
699 tree species resistance, despite the existence of possible trade-offs between  
700 resistance and recovery (Nimmo et al., 2015) and the fact that both metrics  
701 contribute to explaining overall forest resilience (Holling, 1973; Lloret et al.,  
702 2011). Our SEM analysis tends to support the existence of such a trade-off by  
703 showing that resilience and recovery are associated with different edges of the  
704 same functional axis: communities dominated by conservative species (slow  
705 radial growth, high wood density) were more resistant, whereas communi-  
706 ties dominated by fast-growing species (fast radial growth and high height to  
707 diameter ratio) had higher recovery. The effect of diversity on these two met-

708 rics also differed, with resistance being largely driven by functional diversity,  
709 whereas recovery was driven only by species diversity. Overall, resistance  
710 appeared to have the strongest effect on the resilience metric we used, sup-  
711 porting the various studies arguing that resilience is higher in communities  
712 dominated by conservative rather than fast-growing species (Hérault et al.,  
713 2018; White et al., 2023). Our results thus shed light on the fact that resis-  
714 tance and recovery are driven by different processes (Falk et al., 2022), and  
715 on the relative influence of these two metrics on resilience.

716

717 *Simulating forest dynamics from an equilibrium in the context of global*  
718 *change* - In this study, we chose to simulate forest trajectories from a stable  
719 equilibrium, in line with the classical notion of resilience that uses a ref-  
720 erence equilibrium state (Holling, 1973; Lloret et al., 2011; Albrich et al.,  
721 2020). Simulating disturbances from an equilibrium state is also the most  
722 common approach found in similar studies (Morin et al., 2018; Schmitt et al.,  
723 2020; Guyennon et al., 2023), in part because using a reference equilibrium  
724 allows clear quantification of resilience. As the identification of a long-term  
725 equilibrium state is notoriously difficult in field studies due to their limited  
726 temporal range, the use of a reference equilibrium state often involves the use  
727 of a model. In that sense, the study of resilience well illustrates the benefits  
728 of using modeling approaches and the complementarity between modeling  
729 and field studies, despite the limitations that are inherent to all models. In  
730 the present study for instance, our recruitment model was relatively sim-  
731 ple, and the IPM simulations always recovered both in terms of total basal  
732 area and in terms of species composition. Field studies have however shown

733 that storm-induced competition-release can promote a decoupled recovery of  
734 forest structure and species composition (Chin et al., 2023). Furthermore,  
735 while the question of forest response to single disturbance in equilibrium is  
736 a first step to understanding the mechanisms that drive resilience, forests  
737 can in reality take centuries to reach this equilibrium, while the return rate  
738 of disturbances tends to be much lower. This argues for the development  
739 of quantitative approaches to measure resilience in the absence of a strict  
740 equilibrium and in response to disturbance regimes rather than to single dis-  
741 turbances (Seidl et al., 2011). Johnstone et al., 2016 theorized that forest  
742 resilience to disturbance regimes arises from an alignment between the char-  
743 acteristics of these regimes (*i.e.*, disturbance type, frequency, size) and tree  
744 species traits characterizing the response to these disturbances (*e.g.*, fecun-  
745 dity, resistance traits). Under this theory, looking at forest resilience in the  
746 context of changes in disturbance regimes (Senf et al., 2018; Patacca et al.,  
747 2022) in term of basal area but also in term of forest functional composition  
748 will be an important next step.

749

## 750 **6 Conclusion**

751 Our simulation study highlights the key role of tree species composition in  
752 the ability of European forests to both resist and recover from storm dis-  
753 turbance. In particular, we showed that diverse forests dominated by con-  
754 servative rather than fast-growing species are more resilient to storm distur-  
755 bances due to their high resistance. We also showed that the relationship



756 between tree species composition and resilience is highly climate sensitive.  
757 Finally, our results suggest that climate directly and indirectly influences  
758 resilience, with forests from cold and wet climates being less resilient due  
759 to unfavourable growth conditions for recovery and changes in tree species  
760 composition towards less functionally diverse communities. In the context of  
761 intensifying disturbance regimes across all climatic biomes, our simulations  
762 highlight the key interactions between climate, tree species composition and  
763 forest resilience to disturbance, which should help to anticipate the conse-  
764 quences of climate change and intensifying disturbance regimes on forest  
765 ecosystem dynamics.

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#### 1004 **Supporting information**

1005 Additional supporting information may be found in the online version of this

1006 article.  
1007 Appendix A: NFI data for model calibration  
1008 Appendix B: Demographic functions  
1009 Appendix C: Calculation of species-specific time to reach 10cm dbh  
1010 Appendix D: Estimation of demographic stochasticity in the IPM model  
1011 Appendix E: Changes in basal area along a simulation  
1012 Appendix F: Comparison of the change in basal area and in species compo-  
1013 sition  
1014 Appendix G: Description of the structural equation model  
1015 Appendix H: Statistics of the model of hypothesis 1  
1016 Appendix I: Statistics of the model of hypothesis 2  
1017 Appendix J: Statistics of the model of hypothesis 3  
1018 Appendix K: Effect of climate on size structure and species composition sim-  
1019 ulated at equilibrium

1020

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1032

### 1033 **Author contributions**

1034 JB, BR and GK conceived the ideas and designed methodology; GK de-  
1035 veloped the IPM model. MJ developed the code of the model; JB ran the  
1036 simulations, analysed the data and led the writing of the manuscript. All  
1037 authors contributed critically to the drafts and gave final approval for pub-  
1038 lication.

1039

### 1040 **Conflict of interest**

1041 The authors have no conflict of interest to declare.

1042

### 1043 **Statement on inclusion**

1044 Our paper presents a simulation-based study and brings together four au-  
1045 thors of two different nationalities (French and German), all institutionally  
1046 affiliated in France, where the model was developed. France is one of the  
1047 five European countries that contributed data for the model calibration. Al-  
1048 though the contributions of colleagues from Germany, Spain, Sweden and  
1049 Finland were invaluable during the calibration phase, they are not included  
1050 in this specific publication as their work has been adequately recognised in  
1051 two previous papers dedicated to model calibration. Our current study focuses  
1052 primarily on simulations carried out using the calibrated model. Where rel-  
1053 evant, literature published by scientists from the region has also been cited;  
1054 efforts have been made to include relevant work published in the local lan-  
1055 guage. We remain committed to maintaining a spirit of inclusivity in our

1056 research, ensuring that our work remains accessible, representative and sup-  
1057 portive of all voices within our diverse community.

1058

#### 1059 **Data availability statement**

1060 All National Forest Inventory data and climatic data used in this study are  
1061 publicly available, and all the links to download them are provided in the  
1062 supplementary material. The R package *matreex* (Jaunatre *et al.* 2023),  
1063 developed to run simulations with the IPM, is publicly available at [https:](https://github.com/gowachin/matreex)  
1064 [//github.com/gowachin/matreex](https://github.com/gowachin/matreex). The code for all the analyses of this pa-  
1065 per is publicly available at [https://github.com/jbarrere3/FunDiv\\_ipm](https://github.com/jbarrere3/FunDiv_ipm).

1066