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1 **Climate- and successional-related changes in functional composition of European forests**  
2 **are strongly driven by tree mortality**

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47 **Running head:** Functional composition changes in forests

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58 **Abstract**

59 Intense droughts combined with increased temperatures are one of the major threats to forest  
60 persistence in the 21<sup>st</sup> century. Despite the direct impact of climate change on forest growth  
61 and shifts in species abundance, the effect of altered demography on changes in the  
62 composition of functional traits is not well known. We sought to: (1) quantify the recent  
63 changes in functional composition of European forests; (2) identify the relative importance of  
64 climate change, mean climate and forest development for changes in functional composition;  
65 and (3) analyse the roles of tree mortality and growth underlying any functional changes in  
66 different forest types. We quantified changes in functional composition from the 1980s to the  
67 2000s across Europe by two dimensions of functional trait variation: the first dimension was  
68 mainly related to changes in leaf mass per area and wood density (partially related to the trait  
69 differences between angiosperms and gymnosperms), and the second dimension related to  
70 changes in maximum tree height. Our results indicate that climate change and mean climatic  
71 effects strongly interacted with forest development and it was not possible to completely  
72 disentangle their effects. Where recent climate change was not too extreme, the patterns of  
73 functional change generally followed the expected patterns under secondary succession (e.g.  
74 towards late-successional short-statured hardwoods in Mediterranean forests and taller  
75 gymnosperms in boreal forests) and latitudinal gradients (e.g. larger proportion of  
76 gymnosperm-like strategies at low water availability in forests formerly dominated by broad-  
77 leaved deciduous species). Recent climate change generally favoured the dominance of  
78 angiosperm-like related traits under increased temperature and intense droughts. Our results  
79 show functional composition changes over relatively short time scales in European forests.  
80 These changes are largely determined by tree mortality, which should be further investigated  
81 and modelled to adequately predict the impacts of climate change on forest function.

## 82 **Introduction**

83

84 Human-mediated modifications of natural ecosystems are leading to important diversity losses  
85 and changes in species forest composition (Chapin *et al.*, 2000, Cardinale *et al.*, 2012), thus  
86 directly affecting the functions and services provided by forests (Gamfeldt *et al.*, 2013, van der  
87 Plas *et al.*, 2016). During the last decades, changes in mean climate and alterations to climatic  
88 extremes have led to changes in tree demography (Allen *et al.*, 2015), forest productivity (Ruiz-  
89 Benito *et al.*, 2014b) and carbon cycle (Frank *et al.*, 2015). There is a long tradition of studies  
90 analysing how functional traits change along climatic gradients (Díaz *et al.*, 2016). However,  
91 few studies have investigated how temporal changes in functional trait distributions are driven  
92 by changing climatic conditions and quantified potential changes in functional composition  
93 (see Dubuis *et al.*, 2013, Mokany *et al.*, 2015).

94         The effect of climate on community dynamics (i.e. changes in the abundance and  
95 composition of species and functional groups) operates through the modification of population  
96 demographic rates (mainly mortality, growth and regeneration, Oliver & Larson, 1996,  
97 Pretzsch, 2009). Ongoing climate change –particularly intense droughts and increased  
98 temperatures– have already translated into increased tree mortality (Allen *et al.*, 2015), which  
99 may lead to latitudinal and altitudinal changes in forest species distribution (e.g. Benito-Garzón  
100 *et al.*, 2013, Urli *et al.*, 2014). It has been hypothesised that abrupt vegetation shifts may occur  
101 as a consequence of drought-induced mortality: examples range from temperate evergreen  
102 forests (e.g. high vulnerability of *Pinus sylvestris* in south and central Europe, Galiano *et al.*,  
103 2010) to temperate broadleaved forests (e.g. high vulnerability of *Nothofagus dombeyi* in SW  
104 Argentina, Suarez & Kitzberger, 2008). However, changes in community composition due to  
105 increased stress will depend on the individual species' vulnerability to increased drought and  
106 interactions with stand development (Lloret *et al.*, 2012, Reyer *et al.*, 2015).

107           The effect of climate change on forest species composition and functioning might  
108 depend on the functional traits of the dominant species (e.g. Jucker *et al.*, 2014, Ratcliffe *et al.*,  
109 2016, Ruiz-Benito *et al.*, 2016), legacy effects (e.g. past management, disturbance and previous  
110 extreme droughts; Bengtsson *et al.*, 2000, Anderegg *et al.*, 2015, Clark *et al.*, 2016, Perring *et*  
111 *al.*, 2016), and forest succession and development (e.g. Ruiz-Benito *et al.*, 2013, García-Valdés  
112 *et al.*, 2015). The use of functional traits is emerging as a promising approach to study the  
113 impacts of climate change on ecosystem functioning (Suding *et al.*, 2008, Violle *et al.*, 2014),  
114 because alterations in the dominance of key functional traits can be directly linked to changes  
115 in ecosystem functioning (see Table 1). Importantly, co-variation between traits implies that  
116 functional strategies can be described using a few axes of trait variation (Westoby, 1998,  
117 Westoby *et al.*, 2002). In general, angiosperm and gymnosperm species have contrasting  
118 functional traits that can be linked to their different life history strategies and responses to  
119 environmental conditions (Brodribb *et al.*, 2012, Carnicer *et al.*, 2013). It has been suggested  
120 that gymnosperms have a greater ability to withstand abiotic stress (i.e. high persistence) while  
121 angiosperms have a greater competitive ability and tend to dominate in diverse forests (Coomes  
122 *et al.*, 2005, Carnicer *et al.*, 2013). Despite the current evidence from regional to global scales  
123 of increased tree mortality due to higher temperatures and intense droughts (Anderegg *et al.*,  
124 2013), little is known about the actual impact of climate change on changes in forest functional  
125 trait composition. Although differences in drought-induced mortality have been found for  
126 functional trait values of dominant species, differences in mortality are not so easily identifiable  
127 using taxonomic or functional groups (e.g. angiosperms vs. gymnosperm, Anderegg *et al.*,  
128 2016, Greenwood *et al.*, 2016).

129           Here, we quantified recent changes in forest functional composition by investigating  
130 changes in the dominance of five key functional traits using resurveyed data from *c.* 68,000  
131 permanent forest plots including 143 species spanning Mediterranean to temperate and boreal

132 climates. Our objectives were to: (1) quantify the main recent temporal changes in functional  
133 composition of European forests; (2) identify the relative importance of climate change, mean  
134 climate and forest development; and (3) disentangle the roles of tree mortality and growth  
135 underlying any changes in different forest types. To our knowledge, these analyses for the first  
136 time link large-scale spatial changes in forest functional composition with recent temporal  
137 changes in climate, revealing critical information for predicting future changes in species  
138 composition and forest ecosystem function.

## 139 **Materials and methods**

140

### 141 **Inventory platform and study area**

142

143 We compiled data from the National Forest Inventories (NFIs) of Finland, Germany, Spain,  
144 Sweden and Wallonia (Belgium) (see a detailed description in Appendix S1) covering the large  
145 latitudinal gradient of Europe (*c.* 5.000 km). For each tree we compiled information on the  
146 species identity (see Table S1), d.b.h. and status (alive or dead). To select comparable data  
147 from the inventories we only included re-surveyed plots with a basal area equal or greater than  
148 4 m<sup>2</sup> ha<sup>-1</sup> and trees with a minimum d.b.h. of 10 cm in the consecutive surveys; and we only  
149 included plots where the time between surveys was equal to or larger than 5 years (mean =  
150 11.32).

151 European forests cover a large latitudinal and climatic gradient extending from boreal  
152 to temperate and Mediterranean climates (Fig. S1). We classified each plot according to (i) the  
153 abundance of the species depending on leaf type and habit (i.e. broad- vs. needle-leaved,  
154 deciduous vs. evergreen), and (ii) the Mediterranean character of the species (i.e. some species  
155 are restricted to Mediterranean climates, while others are distributed from boreal to temperate  
156 and Sub-Mediterranean biomes, see Table 1). We used this classification because we expected  
157 angiosperm and gymnosperm forests –showing distinct patterns of leaf type: broad-leaved  
158 deciduous or needle-leaved evergreen, respectively– to have different responses to drought and  
159 increased temperature (Brodribb *et al.*, 2012, Carnicer *et al.*, 2013), and the response to climate  
160 may be different in forests specifically adapted to limited water availability (e.g. Grossiord *et*  
161 *al.*, 2014). From the *c.* 68,000 permanent plots, we only considered forest types with more than  
162 1,000 plots: broad-leaved deciduous (15,234 plots), needle-leaved evergreen (32,215 plots),



163 needle-leaved evergreen Mediterranean (9,395 plots) and broad-leaved evergreen  
164 Mediterranean forests (5,550 plots, Fig. S1).

165

### 166 **Patterns of change in functional composition across European forests**

167

168 Functional composition was calculated as the community-level weighted means (i.e. mean  
169 value of each trait in each plot weighted by the relative abundance of each species in basal area  
170 terms; Lavorel *et al.*, 2008). We compiled five traits which were available for c. 95% of the  
171 species (see Table S1): leaf mass per area (LMA, g m<sup>-2</sup>), wood density (WD, g cm<sup>-3</sup>), seed mass  
172 (SM, mg), water potential causing 50% loss of hydraulic conductivity (P50, MPa), and  
173 maximum tree height (MTH, m). Trait information was compiled via the TRY Initiative  
174 (<http://www.try-db.org>; Kattge *et al.*, 2011) and additional references (Table S1). We  
175 quantified changes in functional composition as the absolute annual change in each functional  
176 trait selected instead of a relative change, because it informs well about both the direction of  
177 the change and its magnitude (i.e. positive or negative, and the absolute value of the change,  
178 Fig. S1 and Fig. S2).

179

### 180 **Potential drivers of changes in forest functional composition**

181

182 Each forest inventory plot was characterised by climate, stand development and demographic  
183 rate variables (see Fig. S3). Climate was defined by variables related to a selection of its  
184 components: (i) *mean climate*: potential evapotranspiration (PET, mm), aridity (i.e.  
185 PET/annual precipitation, adimensional), and water availability (i.e. (annual precipitation –  
186 PET)/PET, %), downloaded from CGIAR-CSI GeoPortal (Zomer *et al.*, 2008); (ii) *recent*  
187 *changes in mean climate*: temperature and precipitation anomaly, defined as the difference

188 between the mean temperature or precipitation for the study period (i.e. years between the two  
189 consecutive inventories plus two years before the first survey) and the mean value for the  
190 reference period (1900-2010) in each of the NFI plots ( UDel\_AirT\_Precip data, Boulder,  
191 Colorado, USA); and (iii) *recent climate change due to drought events*: mean SPEI (mean  
192 standardised precipitation-evapotranspiration index value for the period between the inventory  
193 surveys, adimensional), frequency of dry years (i.e. years between the consecutive inventories  
194 with  $\text{SPEI} < 0$ , No. of years), and the most intense drought (a dimension-less index calculated  
195 as the lowest SPEI value between the consecutive inventories); calculated from SPEIbase v2.2.  
196 (Vicente-Serrano *et al.*, 2010). From this list of variables, we selected variables representative  
197 of each of the three components that were not strongly correlated with each other and had low  
198 Variance Inflation Factor (i.e.  $r < 0.6$  and  $\text{VIF} < 4$ , see Dormann *et al.*, 2013): (i) water  
199 availability (WAI, %), (ii) temperature anomaly (TA, C), and (iii) the most intense drought  
200 (ID, adimensional)

201 To represent *stand development*, we selected tree density (No. trees  $\text{ha}^{-1}$ ), mean d.b.h.  
202 (mm) and the functional diversity of each plot. *Functional diversity* was calculated as the  
203 functional dispersion (FD), i.e. the average distance of individual species trait values to the  
204 centroid of the functional trait space of all tree species present in the plot in the first census  
205 based on a presence-absence matrix (Laliberté & Legendre, 2010). We based FD on all five  
206 traits included in the functional composition metric because multiple key traits are desirable to  
207 adequately represent potential niche differences and, therefore, functional diversity (Ruiz-  
208 Benito *et al.*, 2014a, Kraft *et al.*, 2015). Finally, to represent *demography* we used: (i) tree  
209 growth ( $\text{cm}^2 \text{ha}^{-1} \text{yr}^{-1}$ ) calculated as the annual sum of the basal area increment due to growth  
210 of surviving trees and ingrowth; and (ii) tree mortality ( $\text{cm}^2 \text{ha}^{-1} \text{yr}^{-1}$ ) calculated as the annual  
211 basal area lost due to natural mortality between consecutive inventories.

212

## 213 **Statistical analysis**

214

215 The importance of climate, stand development and demography on changes in functional  
216 composition were assessed using three steps. Firstly, we evaluated the change in functional  
217 composition of European forests for each trait separately. As there were strong correlations in  
218 the absolute changes in different functional traits (Fig. S4) we explored the relationship  
219 between the functional traits using a Principal Component Analyses (R Core Team, 2015). We  
220 selected the first two axes of the PCA as representative of the changes in functional  
221 composition, as between them they explained 70% of the variation in the functional changes  
222 (Fig. 1). Secondly, we identified the climatic and forest developmental drivers of changes in  
223 functional composition using linear mixed-effect models. Thirdly, we quantified the effect of  
224 demographic rates on changes in functional composition using piecewise structural equation  
225 models, as these models allow accommodating complex, direct and indirect relationships  
226 between variables that go beyond the simple distinction between explanatory and response  
227 variables. The two latter analyses are explained in more detail in the following sub-sections,  
228 and were repeated including only those plots with no record of recent management to check  
229 for deviations of the patterns observed from models parameterised using all plots (Appendix  
230 S3).

231

## 232 **Changes in functional composition as a function of climate and forest development**

233

234 We modelled changes in functional composition (PC1 and PC2 axes) using linear mixed-  
235 effects models with a normal distribution of residuals. Due to the hierarchical nature of the  
236 sampling (where plots are aggregated in clusters for some countries; see Appendix S1 for more

237 information), we included cluster identity nested in country as a random effect in the model to  
238 account for the lack of independence between the plots.

239         Based on our expectations of climatic and stand developmental effects on the changes  
240 in functional composition, we included seven potential fixed effects (transformed where  
241 necessary to meet assumptions of normality): water availability (WAI, %), temperature  
242 anomaly (TA, C), the most intense drought (ID, adimensional), tree density (TD, log, No. trees  
243 ha<sup>-1</sup>), mean d.b.h. ( $d_m$ , log, mm), functional diversity (FD, sqrt, adimensional), and forest type  
244 (FT, see Fig. S1 and Fig. S3). We tested pair-wise interactions based on our initial hypothesis  
245 of interactive effects between climate and stand development. We also tested the interactions  
246 between climatic variables (i.e.  $WAI \times TA$ ,  $WAI \times ID$ ,  $TA \times ID$ ) to control for the differential  
247 effects of mean climate and recent climate change (Ruiz-Benito *et al.*, 2014b). Forest type was  
248 included as an interaction with all potential fixed effects. All the numerical variables were  
249 examined for outliers and departures from normality; standardised (i.e. the mean was  
250 subtracted from each value and divided by the standard deviation); and the linearity of the  
251 relationships of each predictor with the response variable was later checked (i.e. through partial  
252 residual plots for each predictor variable in the final model) (see Schielzeth, 2010, Ieno & Zuur,  
253 2015).

254         The most parsimonious model was determined using AIC (Akaike Information  
255 Criterion) as an indicator of both parsimony and likelihood (Burnham & Anderson, 2002). To  
256 identify the best-supported model, we compared the full model with candidate models in which  
257 each of the interactions and then each interaction and main effect were removed. We selected  
258 the most complex model that reduced AIC by more than 2 units from the next simplest model  
259 (Hilborn & Mangel, 1997, Burnham & Anderson, 2002). As an indication of relative variable  
260 importance, we report the increase in AIC produced by removing each main effect and  
261 interaction included in the most parsimonious model. The relative importance of each predictor

262 variable was also calculated as the sum of Akaike weight values of the models that contained  
263 that variable from all the potential set of models (i.e. values close to 1 indicate high importance,  
264 Burnham & Anderson, 2002). Finally, parameter estimates and confidence intervals of the best-  
265 supported model were obtained using restricted maximum likelihood (REML), which  
266 minimises the likelihood of the residuals from the fixed-effect portions of the model (Zuur *et*  
267 *al.*, 2009). Pseudo- $R^2$  (proportion of variance explained by both the fixed and random factors)  
268 was used to provide an estimation of variance explained by fixed and random terms (Nakagawa  
269 & Schielzeth, 2013).

270         The predicted changes in functional composition for each forest type and explanatory  
271 variable were computed using the best-supported model, fixing the values of the other  
272 continuous variables at their observed mean (Table 1). These three dimensional predicted  
273 changes were visualised using heat graphs and the actual occurrence of the change in the NFI  
274 data for each forest type was indicated by black lines as a convex hull using *aplpack* library  
275 (Wolf & Bielefeld, 2014). All linear mixed effect models were fitted using *lme4* library (Bates  
276 *et al.*, 2015) and Akaike weights were calculated using *MuMIn* library (Barton, 2016) in R  
277 version 3.2.2. (R Core Team, 2015).

278

### 279 **Demographic drivers of changes in functional composition**

280

281 We conducted piecewise structural equation modelling to test the relative importance of tree  
282 mortality and growth rates on changes in functional composition and to understand how  
283 patterns varied between the forest types, while accounting for the interactive effects of climate  
284 and forest development (see hypotheses in Fig. 2 and Appendix S2 for more details). Piecewise  
285 SEM combines information from multiple separate linear models into a single causal network  
286 and allowed us to incorporate random structures (Shipley, 2009). We used as endogenous

287 variables (i.e. response variables in the separate linear models): (i) forest development, i.e.  
288 mean d.b.h. (mm), tree density (No. trees ha<sup>-1</sup>), and functional diversity; (ii) demography, i.e.  
289 tree growth (log, cm<sup>2</sup> ha<sup>-1</sup> yr<sup>-1</sup>) and tree mortality (log +0.01, cm<sup>2</sup> ha<sup>-1</sup> yr<sup>-1</sup>), because it has been  
290 demonstrated that they both depend on climate and stand development; and (ii) changes in  
291 functional composition quantified as the first two PCA scores of the changes in the five  
292 functional traits.

293         Firstly, we performed a multilevel path analysis (see Appendix S2) for the entire  
294 dataset, including all forest types, which allowed us to detect general trends in the changes in  
295 functional composition related to demography, climate, stand structure and diversity. Pseudo-  
296 R<sup>2</sup> (proportion of variance explained in the model by both the fixed and random factors) was  
297 used to provide an estimation of variance explained (Nakagawa & Schielzeth, 2013). The  
298 analysis was repeated on each forest type separately (i.e. one model per forest type) to identify  
299 any forest type-specific trends. All analyses were conducted in R using the piecewiseSEM  
300 library (Lefcheck, 2015) in R 3.2.0. (R Core Team, 2015).

## 301 **Results**

302

### 303 **Recent patterns of change in functional composition across European forests**

304

305 We analysed absolute changes in each of the five functional traits. Our exploratory analysis  
306 indicated shifts to both positive and negative values for all five traits (i.e. towards larger and  
307 smaller absolute values, respectively, Fig. S1 and S2) but we did not observe any clear spatial  
308 pattern of change (Fig. S5). The results of the PCA performed with the five functional traits  
309 showed that the first axis (PC1, explaining 50% of the variance) was strongly and negatively  
310 correlated with changes in leaf mass per area, and strongly and positively correlated with  
311 changes in wood density (Fig. 1 and Fig. S4). These functional traits are partially associated  
312 with functional strategies that distinguish between angiosperms and gymnosperms: positive  
313 values of PC1 reflect a greater dominance of angiosperm-like strategies (i.e. higher wood  
314 density and lower leaf mass per area, and higher vulnerability to xylem embolism and seed  
315 mass), whereas negative values reflect a greater dominance of gymnosperm-like strategies (i.e.  
316 lower wood density and greater leaf mass per area, see Fig. 1 and Appendix S4). Because of  
317 this association, we compared how the changes in PC1 (hereafter, trait-based approach)  
318 correlated with changes in the proportion of gymnosperms (hereafter, taxonomic-based  
319 approach). Although the relationship was linear (see Appendix S4) the correlation was  
320 relatively low ( $r < 0.4$ ), indicating that changes in functional composition along the PC1 axis  
321 may not always correspond to a change in the proportion of gymnosperms. We also performed  
322 the linear models and the path analyses for the changes in the proportion of gymnosperms as  
323 shown in Appendix S4, allowing us to compare trait-based results with taxonomic-based  
324 results. The second axis of the PCA (PC2, explaining 20% of the variance) was highly and  
325 negatively correlated with changes in maximum tree height (Fig. 1 and Fig. S4). Therefore, the

326 second axis of the PCA relates to the differential competitive ability of species and successional  
327 status (Table 1). We selected the first and second axes of the PCA for our modelling approach  
328 as representative of the major changes in forest functional composition across Europe.

329

### 330 **The interactive effect of climate and forest development drives recent changes in forest** 331 **functional composition**

332

333 Our results indicate interactive effects of climate and forest development on changes in  
334 functional composition, particularly between climate and functional diversity (i.e. both for PC1  
335 and PC2, Table 1). The best models of changes in functional composition based on PC1 and  
336 PC2 included all predictor variables for each forest type (see Table 2, model residuals in Fig.  
337 S6 and Fig. S7 and standardised parameter values in Table S2). In the best model predicting  
338 PC1, the inclusion of variables related to recent climate change was supported, but their  
339 importance was lower than for forest development (see drop in  $\Delta$ AIC in Table 2 when  
340 temperature anomalies and intense droughts were removed from the model). In the best model  
341 predicting PC2, functional diversity and water availability were the most strongly supported  
342 variables (Table 2).

343         Figures 3 and 4 represent the predicted changes in functional composition measured  
344 through PC1 and PC2, respectively, for each forest type (see density plots in Fig. S8 and  
345 relative changes in PC1 in Fig. S9) along gradients of climate (i.e. water availability,  
346 temperature anomaly and drought) and stand development (i.e. density, mean d.b.h. and  
347 diversity). The graphics have been coloured to reflect the magnitude and direction of the change  
348 along the PCA axes. PC1 is related to shifts in functional trait values towards a lower wood  
349 density and higher leaf mass per area (corresponding to the blue colour in Fig. 3 which reflects  
350 positive changes in PC1) or the contrary (red colour in Fig. 3, which reflects negative changes



351 in PC1). PC2 was related to changes in maximum tree height (brown colour in Fig. 4 reflects  
352 a decrease in maximum tree height). The patterns of change predicted using PC1 and PC2 along  
353 climate and stand development gradients, based only on those plots with no record of recent  
354 management, were generally consistent with those observed for all plots (see Appendix S3).

355 In broad-leaved deciduous forests greater shifts towards lower wood density and larger  
356 leaf mass per area (corresponding to red colours in Fig. 3a) occurred where low water  
357 availability (more negative WAI values) coincided with medium-high tree density or mean  
358 d.b.h. (i.e. larger than 300 trees ha<sup>-1</sup> and 200 mm, respectively), where low temperature  
359 anomalies coincided with low tree density (i.e. lower than 0.2 °C and 500 trees ha<sup>-1</sup>,  
360 respectively), and in plots with high functional diversity or under intense droughts (i.e. SPEI  
361 values < -2). At high water availability (WAI > 50%) the models predicted little change in the  
362 functional composition across the entire range of mean diameter and stand densities (Fig. 3a).

363 In needle-leaved evergreen forests the greatest shifts towards greater wood density and lower  
364 leaf mass per area (corresponding to blue colours in Fig. 3c) occurred in plots with low  
365 functional diversity (FD < 0.10), small mean diameter and high water availability and  
366 temperature anomalies (i.e. mean d.b.h. < 200 mm and WAI > 0 or TA > 0.2 °C). In the case  
367 of Mediterranean forests, we found similar patterns for broad- and needle-leaved species.  
368 Changes towards a stronger dominance of individuals with greater wood density and lower leaf  
369 mass per area in Mediterranean forests (i.e. blue colours in Fig. 3b,d) were observed at high  
370 water availability, high temperature anomalies and relatively mild droughts (specially WAI >  
371 0 %, TA > 0.5 °C, and minimum SPEI > -1.5), with higher intensity when tree density and  
372 mean tree diameters are large. The only clear difference between the two forest types was the  
373 interaction between water availability and tree density: Mediterranean broad-leaved forests  
374 tended to change towards larger proportions of species dominated by lower wood density and  
375 greater leaf mass per area at low water availability irrespective of tree density, whereas this

376 pattern was not clear in Mediterranean coniferous forests. The analysis performed on the  
377 change in the proportion of gymnosperms confirmed that most patterns in wood density and  
378 leaf mass per area strongly corresponded to changes between angiosperm and gymnosperm-  
379 dominated stands, but some notable differences were found (see detailed results in Appendix  
380 S4). Particularly, shifts towards a functional group that is different to the dominant group were  
381 more apparent along climatic gradients in the taxonomic-based analysis, especially of  
382 increasing drought (see Fig. S4.4 in Appendix S4).

383 PC2 was related to changes in maximum tree height (Fig. 1). The strongest interactions  
384 between climate and stand development on changes in PC2 occurred in Mediterranean needle-  
385 leaf evergreen forests followed by broad-leaved deciduous forests (Fig. 4). In Mediterranean  
386 conifers most of the changes were towards increases in maximum tree height (i.e. negative  
387 values of PC2), especially at high functional diversity and medium to high tree density and  
388 mean d.b.h., and under intense droughts (Fig. 4d). The same patterns of change towards greater  
389 maximum tree height were observed in broad-leaved deciduous forests, except in areas with  
390 high water availability and temperature anomaly (Fig. 4c).

391

### 392 **Mortality and growth effects on recent changes in functional composition**

393

394 Overall, tree mortality had a larger effect on changes in functional composition than tree growth  
395 (i.e. PC1 and PC2, see standardised effect sizes in Fig. 5), although the ability of the underlying  
396 linear models to explain growth was greater than for mortality models (see  $R^2$  for growth and  
397 mortality models = 0.58, 0.41, respectively; Fig. 5). The effect of mortality was particularly  
398 strong and positive on PC1, which reflected a general change towards strategies with lower  
399 leaf mass per area and higher wood density, seed mass and water potential loss, similar to the  
400 observed changes in the proportion of gymnosperms and plots with no evidence of recent

401 management (see Appendix S3 and S4). For PC2 the mortality effect was negative and the  
402 magnitude was less strong, which reflected a weak increase in maximum tree heights.  
403 Furthermore, we found that the sign of the relationship between mortality and growth on  
404 changes in functional composition was consistent for all the forest types studied (see sign of  
405 standardised parameters in Appendix S2). The strongest effect of mortality on PC1 and PC2  
406 was found in Mediterranean conifers (see magnitude of standardised parameters in Appendix  
407 S2).

408 **Discussion**

409 Our results suggest that recent climate change –i.e. both increased temperature and intense  
410 droughts– are critical drivers of recent changes in the functional composition of European  
411 forests. Overall, the importance of the interaction between climate and forest development  
412 agrees with previous studies that identified similar strong interactions for tree growth (e.g.  
413 Gómez-Aparicio *et al.*, 2011, Ruiz-Benito *et al.*, 2015), tree mortality (e.g. Vilà-Cabrera *et al.*,  
414 2011, Ruiz-Benito *et al.*, 2013), recruitment (e.g. Carnicer *et al.*, 2014, Zhang *et al.*, 2015) and  
415 total changes in basal area and carbon storage (Vayreda *et al.*, 2012, Ruiz-Benito *et al.*, 2014b).  
416 We found that the interactive nature of the drivers underlying changes in functional  
417 composition was due to differential tree demography (Clark *et al.*, 2014, Zhang *et al.*, 2015),  
418 and that it appears to critically depend on tree mortality rates (Allen *et al.*, 2015).

419 We were unable to distinguish whether the changes in functional composition observed  
420 are ultimately driven by anthropogenic and/or natural causes. In Europe, most forests have been  
421 managed and 12% of the forests are planted (FAO, 2006a,b, McGrath *et al.*, 2015). Ultimately,  
422 forest management has largely determined both species selection and structural conditions. A  
423 clear example can be found in boreal forests, where *Picea abies* has been favoured in very  
424 fertile sites and *Pinus sylvestris* in relatively poor sites, and most monospecific forests are  
425 located on private lands (see e.g. FAO, 2006b, Rantala, 2011). In European forests, certain  
426 species might be outside their climatic and structural optimum (e.g. forest planted beyond their  
427 natural distributions and/or densities, see e.g. Ruiz-Benito *et al.*, 2012). However, it is  
428 important to study forest dynamics across climatic gradients in Europe, regardless of their  
429 origin and management history, because it is likely that all will be impacted by climate change  
430 to some degree. Our focus at the continental scale allows us to detect large-scale changes that  
431 could be useful for national conservation and management plans.

432 Here, we summarised the changes in functional composition through the variation in  
433 two-dimensional axes of change related to: (i) the functional strategies of the species, reflecting  
434 differences in a continuum of traits from high leaf mass per area and low wood density to low  
435 leaf mass per area and high wood density; and (ii) maximum tree height. Overall, the two axes  
436 of variation are in line with the Leaf-Height-Seed scheme (Westoby, 1998), which captures  
437 variation in functional traits while considering the importance of stem density for woody plants  
438 (Chave *et al.*, 2009, Reich, 2014). These axes of variation reflect the two dominant strategies  
439 of gymnosperms and angiosperms (Stahl *et al.*, 2014) and correspond to the major trends of  
440 variation found in plant forms worldwide (Díaz *et al.*, 2016). The first axis (leaf mass – wood  
441 density) is a good predictor of resource use and responses to environmental conditions (Table  
442 1). Although the change in functional composition using PC1 axis corresponds partially to a  
443 taxonomic change towards a greater proportion of gymnosperms (Appendix S4), our trait-  
444 based approach allowed us to further understand the conserved patterns given the substantial  
445 overlap of trait values across communities between and within functional groups. This is  
446 consistent with recent meta-analyses showing that trait-based approaches are able to better  
447 identify drought-induced tree mortality patterns than taxonomic-based approaches (Anderegg  
448 *et al.* 2016; Greenwood *et al.* 2016). The second axis (maximum tree height) is strongly related  
449 to the differential competitive ability of the species and, therefore, to the successional progress  
450 of each forest stand (Table 1). Although changes in each functional trait can be highly  
451 informative we selected the PCA axes for an overall understanding of community-level  
452 functional changes, which is needed to further manage ecosystems and understand potential  
453 effects of climate change (see e.g. de Bello *et al.*, 2010).

454

455 **Climate change impacts on recent changes in functional strategies across European**  
456 **forests**

457

458 We observed that recent climate change, via increases in temperature and intense droughts, is  
459 leading to directional changes across European forests, but these changes are also dependent  
460 on forest development, and the corresponding changes in tree density, size and diversity. In  
461 relatively well-developed mature forests (i.e. tree densities and mean tree diameter larger than  
462 500 trees ha<sup>-1</sup> and 200 mm, respectively) with temperature anomalies higher than 0.2 °C we  
463 found a change towards a greater proportion of individuals with high wood densities and low  
464 leaf mass per area in broadleaved forests and Mediterranean conifers. Our observation that  
465 gymnosperms could be vulnerable to increases in temperature and water stress is consistent  
466 with recent studies that reported or predicted high mortality in conifers (McDowell and Allen,  
467 2015, McDowell *et al.*, 2016), and studies suggesting that warming could be promoting  
468 climatic conditions more favourable for angiosperms (e.g. Henne *et al.*, 2015, McIntyre *et al.*,  
469 2015). Recent meta-analyses did not find clear differences between angiosperm and  
470 gymnosperm mortality responses to drought, despite clear trait-level differences in specific leaf  
471 area, wood density or hydraulic traits (Anderegg *et al.*, 2016; Greenwood *et al.*, 2016).  
472 However, we cannot discount the possibility that the observed functional changes towards a  
473 greater proportion of angiosperm-like strategies under increased temperature may be coupled  
474 to land-use changes promoting an increase in the relative abundance of oaks and other  
475 hardwoods (Carnicer *et al.*, 2014, Henne *et al.*, 2015, Vayreda *et al.*, 2016). In fact, the  
476 observed increase in the proportion of angiosperms might have been favoured by relatively  
477 recent processes that affect secondary succession, such as agricultural abandonment and  
478 changes in management practices –e.g. coppicing, charcoal production– (Barberó *et al.*, 1998,  
479 Urbietta *et al.*, 2008, Müllerová *et al.*, 2015).

480

Intense droughts led to changes towards functional traits values different from the  
481 dominant group in all forest types with mean tree diameter < 400 mm, and this was even more

482 distinct when assessed as changes in the proportion of gymnosperms (Appendix S4).  
483 Furthermore, this change was not observed in conifers of small-medium diameter (i.e. mean  
484 d.b.h. < 400 mm) and at low diversity (Fig. 3). The shift in the dominant functional strategy in  
485 broad-leaved evergreen forests under intense droughts at large diameters is in accordance with  
486 previous studies that suggest trade-offs between plant size and drought tolerance (i.e. Ryan *et*  
487 *al.*, 2006, Moles *et al.*, 2009, Bennett *et al.*, 2015). This change towards traits linked to  
488 gymnosperm-like strategies could be due to the highest mortality or lowest growth of the most  
489 dominant functional strategy in relatively mature forests, because all species are likely to be  
490 stressed if the drought is very extreme and water availability is limiting (Choat *et al.*, 2012).

491

492 **Patterns of change in functional strategies and maximum tree height reflect expected**  
493 **patterns of change due to secondary succession and biogeography**

494

495 The recent changes in functional composition linked to leaf mass per area and wood density,  
496 and corresponding functional strategies (i.e. changes in PC1 and proportion of gymnosperms,  
497 respectively) across Europe were strongly dependent on functional diversity. The influence of  
498 diversity was strong when compared to climatic variables, leading to clear patterns of change  
499 in all forest types (Fig. 3). Areas of low tree diversity and monospecific forests might  
500 correspond with planted-forests, which in many cases are planted outside their natural climatic  
501 range even when they are composed of native species (e.g. Ruiz-Benito *et al.* 2012). At high  
502 diversity levels in Mediterranean forests, we found greater shifts towards a larger dominance  
503 of individuals with greater wood density, lower leaf mass per area and, overall, angiosperm-  
504 like strategies. In contrast, diverse temperate and boreal forests tended to change towards a  
505 larger dominance of greater leaf mass per area, lower wood density and gymnosperm-like  
506 strategies. The trends predicted with increasing functional diversity are consistent with the

507 expectations of the secondary successional trajectory expected in the different forest types or  
508 regions, which in Mediterranean forests generally leads to a greater dominance of late-  
509 successional hardwoods (Zavala & Zea, 2004, Carnicer *et al.*, 2014, Vayreda *et al.*, 2016). In  
510 contrast, forests distributed in boreal European biomes are generally changing towards a greater  
511 dominance of late-successional conifers (e.g. Angelstam & Kuuluvainen, 2004, Ratcliffe *et al.*,  
512 2016). The change towards a greater dominance of gymnosperms at high diversity could also  
513 be due to the relatively higher growth rates of co-existing conifers when compared to slow-  
514 growing angiosperms, despite their lower competitive ability (e.g. Zavala *et al.*, 2000, Coomes  
515 *et al.*, 2005).

516         The observed shifts in functional strategies along the latitudinal gradient of Europe (i.e.  
517 delineated by water availability, Fig. S1 and S3) agree with the expected biogeographical  
518 patterns of each forest type. Changes towards the most dominant functional trait values in each  
519 forest type occur where water is not too limiting (Fig. 3), which might imply that water  
520 availability is acting as a species filter at the continental scale (e.g. Šímová *et al.*, 2015). Firstly,  
521 in broad-leaved forests at low water availabilities we found the greatest change towards a  
522 greater dominance of species with low wood density and high leaf mass per area, suggesting  
523 increased growth of fast-growing strategies (i.e. gymnosperm-like strategies) and higher  
524 mortality of slow-growing strategies (i.e. angiosperm-like strategies, Fig. 3a,b and Appendix  
525 S4). At the rear edge of broad-leaved temperate forests (i.e. generally related to low water  
526 availability) an altered demography, with growth declines and mortality increases, could be  
527 driving the observed changes in functional strategies (Hampe & Petit, 2005, Jump *et al.*, 2006).  
528 Secondly, in conifers we found a larger transition towards angiosperm strategies at low water  
529 availability, which might be reflecting the expected altitudinal and latitudinal transition  
530 (Benito-Garzón *et al.*, 2013). Thirdly, in Mediterranean forests at high water availability we  
531 found shifts in functional composition towards a greater proportion of angiosperms, which



532 agrees with observed recruitment trends along the Iberian Peninsula and it follows the expected  
533 advance of secondary succession (Vayreda *et al.*, 2013, Carnicer *et al.*, 2014, Vayreda *et al.*,  
534 2016).

535 Many of the changes along climatic and forest development gradients were related to  
536 increases in maximum tree height (see green colours in Fig. 4). Functional diversity and water  
537 availability were the main drivers of the changes in maximum tree height, particularly in broad-  
538 leaved and Mediterranean coniferous forests. At high diversity we found generally an increase  
539 in maximum tree height (see also Marks *et al.*, 2016), which might be reflecting the expected  
540 secondary succession trajectory. In wet sites (i.e. water availability > 0), we found that  
541 Mediterranean conifer forests (i.e. maximum height *c.* 28 m, see Fig. S10) tended to shift  
542 towards a higher dominance of tall species at high diversity, which agrees with the successional  
543 change expected towards broad-leaved deciduous species (e.g. *Fagus sylvatica*, *Quercus robur*,  
544 *Q. petraea* and *Castanea sativa*; with maximum tree height of *c.* 41 m, (Rivas-Martínez, 1987,  
545 Costa *et al.*, 1997). In areas of low water availability and mild drought, changes towards shorter  
546 statured trees could be reflecting a transition towards Mediterranean and Sub-Mediterranean  
547 species (e.g. with maximum height of *c.* 19 m for *Q. ilex* and *Q. suber*; and *c.* 24 m for *Q.*  
548 *faginea* and *Q. pyrenaica*, see Fig. S10). The transition between Mediterranean conifers and  
549 oaks is typical of the drier end of the water availability gradient, where a shifting mosaic  
550 between pines and oaks depends on management and landscape heterogeneity (Zavala *et al.*,  
551 2000, Zavala & Zea, 2004), in agreement with the current and past co-dominance of these two  
552 groups in the Mediterranean from paleo-ecological data (Carrion *et al.*, 2001).

553

#### 554 **The role of demography underlying changes in functional composition**

555

556 Our results suggest a critical role of tree mortality when compared to tree growth for changes  
557 in the functional composition of European forests undergoing secondary succession, which  
558 agrees with previous studies conducted from tropical to temperate and boreal forests (van  
559 Mantgem & Stephenson, 2007, Lasky *et al.*, 2014, Zhang *et al.*, 2015). Due to limitations  
560 combining data from different inventories we focused on adult trees with d.b.h. > 10 cm, but  
561 we acknowledge that tree regeneration plays a key role in long-term forest dynamics and it  
562 could be highly vulnerable to climate change effects (e.g. Zhu *et al.*, 2012). Furthermore, we  
563 are working with permanent forest plots along the entire European continent in which we could  
564 not analyse the effect of other global change drivers –e.g. land use change, nitrogen deposition  
565 or extreme fires, storms or droughts– that might further drive changes in forest structure and  
566 composition beyond certain thresholds (e.g. Frank *et al.*, 2015; Jump *et al.*, 2016). However,  
567 we have identified tree mortality as a key driver of three patterns of change in the functional  
568 strategies observed across European forests. Firstly, increased mortality of species with low  
569 wood density and high leaf mass per area (see also Greenwood *et al.*, 2016, McDowell and  
570 Allen, 2015) could be driving changes towards a greater dominance of angiosperm-like  
571 functional traits across Europe particularly under high temperature anomalies in all forest types  
572 and under intense droughts in mature needle-leaved forests. Secondly, increased mortality of  
573 broadleaved species at the dry edge of temperate species broadly distributed across Europe (i.e.  
574 at low water availability) may be leading to a greater dominance of gymnosperms at the rear  
575 edge of broad-leaved deciduous forests, as for example those forests dominated by *Fagus*  
576 *sylvatica* or *Quercus robur* (Peñuelas *et al.*, 2013). Finally, the change towards a larger  
577 proportion of angiosperms in Mediterranean forests with tree densities and mean diameter  
578 larger than 500 trees ha<sup>-1</sup> and 200 mm, respectively, and not strongly limited by water  
579 availability, agrees with the greater role of mortality relative to growth in forests undergoing  
580 secondary succession, and might be associated with recent changes in forest management

581 across Europe. This change could be due to the fact that pioneer species (i.e. conifers generally  
582 characterised by low wood density and high leaf mass per area) tend to show the highest growth  
583 rates (Ratcliffe *et al.*, 2016) but also the highest mortality rates (Benito-Garzón *et al.*, 2013,  
584 Ruiz-Benito *et al.*, 2013, Reich, 2014), leading to changes towards a larger proportion of  
585 angiosperms, as expected in Mediterranean climates (Urbieto *et al.*, 2008, Henne *et al.*, 2015).

586

## 587 **Conclusions and implications**

588

589 Overall, we found that changes in functional composition in European forests can be  
590 characterised along two axes of variation summarising leaf-wood traits, on the one hand, and  
591 maximum height on the other. We found that most climatic and forest developmental  
592 conditions lead to functional changes in accordance with forest successional pathways.  
593 However, we found that recent climate change –i.e. increased temperature and intense  
594 droughts– might lead to different pathways of changes in functional strategies than those  
595 expected only from succession. We conclude that increased tree mortality is driving changes  
596 in functional strategies and maximum tree height, which is leading to quantifiable changes in  
597 the functional composition of European forests, despite our greater ability to explain growth  
598 than mortality (Fig. 5). Our study suggests that climatic and forest developmental interactions  
599 are critical to adequately predict forest functional responses under climate change (van  
600 Bodegom *et al.*, 2014). Further studies are essential in order to better understand drivers of tree  
601 mortality and link changes in plant functional traits to ecosystem functioning (Reichstein *et al.*,  
602 2014, Funk *et al.*, 2016) and drought effects to secondary succession and stand development  
603 (Clark *et al.*, 2016).

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605

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627 **REFERENCES**

- 628 Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to  
629 tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, **6**, 129.
- 630 Anderegg WRL, Kane JM, Anderegg LDL (2013) Consequences of widespread tree mortality  
631 triggered by drought and temperature stress. *Nature Climate Change*, **3**, 30-36.
- 632 Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S (2016) Meta-  
633 analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree  
634 mortality across the globe. *Proceedings of the National Academy of Sciences*, **113**, 5024-5029.
- 635 Anderegg WRL, Schwalm C, Biondi F *et al.* (2015) Pervasive drought legacies in forest  
636 ecosystems and their implications for carbon cycle models. *Science*, **349**, 528-532.
- 637 Angelstam P, Kuuluvainen T (2004) Boreal forest disturbance regimes, successional dynamics  
638 and landscape structures – a European perspective. *Ecological Bulletins*, **51**, 117-136.
- 639 Barberó M, Loisel R, Quézel P, Richardson DM, Romane F (1998) Pines of the Mediterranean  
640 basin. In: *Ecology and biogeography of Pinus*. (ed Richardson DM) pp Page. Cambridge,  
641 Cambridge University Press.
- 642 Bartom, K (2016) MuMIn: Multi-Model Inference. R package version 1.15.6. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)  
643 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 644 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using  
645 lme4. *Journal of Statistical Software*, **67**, 1-48.
- 646 Bengtsson J, Nilsson SG, Franc A, Menozzi P (2000) Biodiversity, disturbances, ecosystem  
647 function and management of European forests. *Forest Ecology and Management*, **132**, 39-50.
- 648 Benito-Garzón M, Ruiz-Benito P, Zavala MA (2013) Inter-specific differences in tree growth  
649 and mortality responses to climate determine potential species distribution limits in Iberian  
650 forests. *Global Ecology and Biogeography*, **22**, 1141-1151.
- 651 Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ (2015) Larger trees suffer most  
652 during drought in forests worldwide. *Nature Plants*, **1**, 15139.
- 653 Brodribb TJ, Pittermann J, Coomes DA (2012) Elegance versus speed: examining the  
654 competition between conifer and angiosperm trees. *International Journal of Plant Sciences*,  
655 **173**, 673-694.
- 656 Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical*  
657 *information-theoretic approach*, New York, Springer-Verlag.
- 658 Cardinale BJ, Duffy JE, Gonzalez A *et al.* (2012) Biodiversity loss and its impact on humanity.  
659 *Nature*, **486**, 59-67.

- 660 Carnicer J, Barbeta A, Sperlich D, Coll M, Penuelas J (2013) Contrasting trait syndromes in  
661 angiosperms and conifers are associated with different responses of tree growth to temperature  
662 on a large scale. *Frontiers in Plant Science*, **4**.
- 663 Carnicer J, Coll M, Pons X, Ninyerola M, Vayreda J, Peñuelas J (2014) Large-scale recruitment  
664 limitation in Mediterranean pines: the role of *Quercus ilex* and forest successional advance as  
665 key regional drivers. *Global Ecology and Biogeography*, **23**, 371-384.
- 666 Carrion JS, Andrade A, Bennett KD, Navarro C, Munuera M (2001) Crossing forest thresholds:  
667 inertia and collapse in a Holocene sequence from south-central Spain. *Holocene*, **11**, 635-653.
- 668 Chapin FS (2003) Effects of plant traits on ecosystem and regional processes: a conceptual  
669 framework for predicting the consequences of global change. *Annals of Botany*, **91**, 455-463.
- 670 Chapin FS, Zavaleta ES, Eviner VT *et al.* (2000) Consequences of changing biodiversity.  
671 *Nature*, **405**, 234-242.
- 672 Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a  
673 worldwide wood economics spectrum. *Ecology Letters*, **12**, 351-366.
- 674 Choat B, Jansen S, Brodribb TJ *et al.* (2012) Global convergence in the vulnerability of forests  
675 to drought. *Nature*, **491**, 752-755.
- 676 Clark JS, Bell DM, Kwit MC, Zhu K (2014) Competition-interaction landscapes for the joint  
677 response of forests to climate change. *Global Change Biology*, **20**, 1979-1991.
- 678 Clark JS, Iverson L, Woodall CW *et al.* (2016) The impacts of increasing drought on forest  
679 dynamics, structure, and biodiversity in the United States. *Global Change Biology*, **22**, 2329-  
680 2352.
- 681 Coomes DA, Allen RB, Bentley WA *et al.* (2005) The hare, the tortoise and the crocodile: the  
682 ecology of angiosperm dominance, conifer persistence and fern filtering. *Journal of Ecology*,  
683 **93**, 918-935.
- 684 Costa M, Morla C, Sáinz H (1997) *Los bosques ibéricos: una interpretación geobotánica*,  
685 Barcelona, Editorial Planeta.
- 686 De Bello F, Lavorel S, Díaz S *et al.* (2010) Towards an assessment of multiple ecosystem  
687 processes and services via functional traits. *Biodiversity and Conservation*, **19**, 2873-2893.
- 688 Díaz S, Hodgson JG, Thompson K *et al.* (2004) The plant traits that drive ecosystems: evidence  
689 from three continents. *Journal of Vegetation Science*, **15**, 295-304.
- 690 Díaz S, Kattge J, Cornelissen JHC *et al.* (2016) The global spectrum of plant form and function.  
691 *Nature*, **529**, 167-171.
- 692 Dormann CF, Elith J, Bacher S *et al.* (2013) Collinearity: a review of methods to deal with it  
693 and a simulation study evaluating their performance. *Ecography*, **36**, 27-46.

- 694 Dubuis A, Rossier L, Pottier J, Pellissier L, Vittoz P, Guisan A (2013) Predicting current and  
695 future spatial community patterns of plant functional traits. *Ecography*, **36**, 1158-1168.
- 696 FAO (2006a) Global forest resource assessment 2005. Food and Agriculture Organization of  
697 the United Nations, Rome.
- 698 FAO (2006b) Global planted forests thematic study. Results and analysis. Food and Agriculture  
699 Organization of the United Nations, Rome.
- 700 Frank D, Reichstein M, Bahn M *et al.* (2015) Effects of climate extremes on the terrestrial  
701 carbon cycle: concepts, processes and potential future impacts. *Global Change Biology*, **21**,  
702 2861-2880.
- 703 Funk JL, Larson JE, Ames GM *et al.* (2016) Revisiting the Holy Grail: using plant functional  
704 traits to understand ecological processes. *Biological Reviews*, n/a-n/a.
- 705 Galiano L, Martínez-Vilalta J, Lloret F (2010) Drought-induced multifactor decline of scots  
706 pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak  
707 species. *Ecosystems*, **13**, 978-991.
- 708 Gamfeldt L, Snäll T, Bagchi R *et al.* (2013) Higher levels of multiple ecosystem services are  
709 found in forests with more tree species. *Nature Communications*, **4**, 1340.
- 710 García-Valdés R, Gotelli NJ, Zavala MA, Purves DW, Araújo MB (2015) Effects of climate,  
711 species interactions, and dispersal on decadal colonization and extinction rates of Iberian tree  
712 species. *Ecological Modelling*, **309–310**, 118-127.
- 713 Gómez-Aparicio L, García-Valdés R, Ruiz-Benito P, Zavala MA (2011) Disentangling the  
714 relative importance of climate, size and competition on tree growth in Iberian forests:  
715 implications for management under global change. *Global Change Biology*, **17**, 2400-2414.
- 716 Greenwood S, Ruiz-Benito P, Martínez-Vilalta J *et al.* (2017) Tree mortality across biomes is  
717 promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology*  
718 *Letters*, **20**, 539-553.
- 719 Grossiord C, Granier A, Ratcliffe S *et al.* (2014) Tree diversity does not always improve  
720 resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences*,  
721 **111**, 14812-14815.
- 722 Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters.  
723 *Ecology Letters*, **8**, 461-467.
- 724 Henne PD, Elkin C, Franke J *et al.* (2015) Reviving extinct Mediterranean forest communities  
725 may improve ecosystem potential in a warmer future. *Frontiers in Ecology and the*  
726 *Environment*, **13**, 356-362.

- 727 Hilborn R, Mangel M (1997) *The ecological detective: confronting models with data*,  
728 Princeton, NJ, USA, Princeton University Press.
- 729 Jump AS, Ruiz-Benito P, Greenwood S *et al.* (2017) Structural overshoot of tree growth with  
730 climate variability and the global spectrum of drought induced forest die-back. *Global Change*  
731 *Biology*.
- 732 Ieno EN, Zuur AF (2015) *Beginner's guide to data exploration and visualization with R*, United  
733 Kingdom, Highland Statistics Ltd.
- 734 Jucker T, Bouriaud O, Avacaritei D, Dănilă I, Duduman G, Valladares F, Coomes DA (2014)  
735 Competition for light and water play contrasting roles in driving diversity–productivity  
736 relationships in Iberian forests. *Journal of Ecology*, **102**, 1202-1213.
- 737 Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the  
738 southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163-2174.
- 739 Kattge J, Díaz S, Lavorel S *et al.* (2011) TRY – a global database of plant traits. *Global Change*  
740 *Biology*, **17**, 2905-2935.
- 741 Kraft NJB, Godoy O, Levine JM (2015) Plant functional traits and the multidimensional nature  
742 of species coexistence. *Proceedings of the National Academy of Sciences*, **112**, 797-802.
- 743 Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity  
744 from multiple traits. *Ecology*, **91**, 299-305.
- 745 Lasky JR, Uriarte M, Boukili VK, Chazdon RL (2014) Trait-mediated assembly processes  
746 predict successional changes in community diversity of tropical forests. *Proceedings of the*  
747 *National Academy of Sciences*, **111**, 5616-5621.
- 748 Lavorel S, Grigulis K, McIntyre S *et al.* (2008) Assessing functional diversity in the field –  
749 methodology matters! *Functional Ecology*, **22**, 134-147.
- 750 Lefcheck JS (2015) piecewiseSEM: Piecewise structural equation modeling in R for ecology,  
751 evolution, and systematics. arXiv, 1509-1845.
- 752 Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012) Extreme climatic  
753 events and vegetation: the role of stabilizing processes. *Global Change Biology*, **18**, 797-805.
- 754 Marks CO, Muller-Landau HC, Tilman D (2016) Tree diversity, tree height and environmental  
755 harshness in eastern and western North America. *Ecology Letters*, **19**, 743-751.
- 756 McGrath MJ, Luysaert S, Meyfroidt P *et al.* (2015) Reconstructing European forest  
757 management from 1600 to 2010. *Biogeosciences*, **12**, 4291-4316.
- 758 McDowell NG, Allen CD (2015) Darcy's law predicts widespread forest mortality under  
759 climate warming. *Nature Climate Change*, **5**, 669-672.



- 760 Mcdowell NG, Williams AP, Xu C *et al.* (2016) Multi-scale predictions of massive conifer  
761 mortality due to chronic temperature rise. *Nature Climate Change*, **6**, 295-300.
- 762 McIntyre PJ, Thorne JH, Dolanc CR, Flint AL, Flint LE, Kelly M, Ackerly DD (2015)  
763 Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and  
764 increased dominance of oaks. *Proceedings of the National Academy of Sciences*, **112**, 1458-  
765 1463.
- 766 Mokany K, Thomson JJ, Lynch AJJ, Jordan GJ, Ferrier S (2015) Linking changes in  
767 community composition and function under climate change. *Ecological Applications*, **25**,  
768 2132-2141.
- 769 Moles AT, Warton DI, Warman L *et al.* (2009) Global patterns in plant height. *Journal of*  
770 *Ecology*, **97**, 923-932.
- 771 Müllerová J, Hédli R, Szabó P (2015) Coppice abandonment and its implications for species  
772 diversity in forest vegetation. *Forest Ecology and Management*, **343**, 88-100.
- 773 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from  
774 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-142.
- 775 Oliver CD, Larson BC (1996) *Forest stand dynamics*, New York, John Wiley & Sons.
- 776 Peñuelas J, Sardans J, Estiarte M *et al.* (2013) Evidence of current impact of climate change  
777 on life: a walk from genes to the biosphere. *Global Change Biology*, **19**, 2303-2338.
- 778 Perring MP, De Frenne P, Baeten L *et al.* (2016) Global environmental change effects on  
779 ecosystems: the importance of land-use legacies. *Global Change Biology*, **22**, 1361-1371.
- 780 Pretzsch H (2009) *Forest dynamics, growth and yield: from measurement to model*, Berlin  
781 Heidelberg, Springer-Verlag.
- 782 R Core Team (2015) R: A language and environment for statistical computing. pp Page,  
783 Vienna, R Foundation for Statistical Computing.
- 784 Rantala S (2011) Finnish forestry practice and management. *Metsäkustannus*. Helsinki,  
785 Finland.
- 786 Ratcliffe S, Liebergesell M, Ruiz-Benito P *et al.* (2016) Modes of functional biodiversity  
787 control on tree productivity across the European continent. *Global Ecology and Biogeography*,  
788 **25**, 251-262.
- 789 Reich PB (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.  
790 *Journal of Ecology*, **102**, 275-301.
- 791 Reichstein M, Bahn M, Mahecha MD, Kattge J, Baldocchi DD (2014) Linking plant and  
792 ecosystem functional biogeography. *Proceedings of the National Academy of Sciences*, **111**,  
793 13697-13702.

- 794 Reyer CPO, Rammig A, Brouwers N, Langerwisch F (2015) Forest resilience, tipping points  
795 and global change processes. *Journal of Ecology*, **103**, 5-15.
- 796 Rivas-Martínez S (1987) *Memoria del mapa de series de vegetación de España*, Madrid.
- 797 Ruiz-Benito P, Gómez-Aparicio L, Paquette A, Messier C, Kattge J, Zavala MA (2014a)  
798 Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and*  
799 *Biogeography*, **23**, 311-322.
- 800 Ruiz-Benito P, Gómez-Aparicio L, Zavala MA (2012) Large scale assessment of regeneration  
801 and diversity in Mediterranean planted pine forests along ecological gradients. *Diversity and*  
802 *Distributions*, **18**, 1092–1106.
- 803 Ruiz-Benito P, Lines ER, Gómez-Aparicio L, Zavala MA, Coomes DA (2013) Patterns and  
804 drivers of tree mortality in Iberian forests: climatic effects are modified by competition. *PLoS*  
805 *ONE*, **8**, e56843.
- 806 Ruiz-Benito P, Madrigal-González J, Ratcliffe S *et al.* (2014b) Stand structure and recent  
807 climate change constrain stand basal area change in European forests: a comparison across  
808 boreal, temperate and Mediterranean biomes. *Ecosystems*, **17**, 1439-1454.
- 809 Ruiz-Benito P, Madrigal-González J, Young S *et al.* (2015) Climatic stress during stand  
810 development alters the sign and magnitude of age-related growth responses in a subtropical  
811 mountain pine. *PLoS ONE*, **10**, e0126581.
- 812 Ruiz-Benito P, Ratcliffe S, Jump AS *et al.* (2017) Functional diversity underlies demographic  
813 responses to environmental variation across European forests. *Global Ecology and*  
814 *Biogeography*, **26**, 128-141.
- 815 Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. *Plant,*  
816 *Cell & Environment*, **29**, 367-381.
- 817 Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients.  
818 *Methods in Ecology and Evolution*, **1**, 103-113.
- 819 Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, **90**,  
820 363-368.
- 821 Shipley B (2013) The AIC model selection method applied to path analytic models compared  
822 using a d-separation test. *Ecology*, **94**, 560-564.
- 823 Šímová I, Violle C, Kraft NJB *et al.* (2015) Shifts in trait means and variances in North  
824 American tree assemblages: species richness patterns are loosely related to the functional  
825 space. *Ecography*, **38**, 649-658.

- 826 Stahl U, Kattge J, Reu B, Voigt W, Ogle K, Dickie J, Wirth C (2014) Whole-plant trait spectra  
827 of North American woody plant species reflect fundamental ecological strategies. *Ecosphere*,  
828 **4**, 2150-8925.
- 829 Suarez MaL, Kitzberger T (2008) Recruitment patterns following a severe drought: long-term  
830 compositional shifts in Patagonian forests. *Canadian Journal of Forest Research*, **38**, 3002-  
831 3010.
- 832 Suding KN, Lavorel S, Chapin FS *et al.* (2008) Scaling environmental change through the  
833 community-level: a trait-based response-and-effect framework for plants. *Global Change*  
834 *Biology*, **14**, 1125-1140.
- 835 Urbieto IR, Zavala MA, Marañón T (2008) Human and non-human determinants of forest  
836 composition in southern Spain: evidence of shifts towards cork oak dominance as a result of  
837 management over the past century. *Journal of Biogeography*, **35**, 1688-1700.
- 838 Urli M, Delzon S, Eyermann A, Couallier V, García-Valdés R, Zavala MA, Porté AJ (2014)  
839 Inferring shifts in tree species distribution using asymmetric distribution curves: a case study  
840 in the Iberian mountains. *Journal of Vegetation Science*, **25**, 147-159.
- 841 Van Bodegom PM, Douma JC, Verheijen LM (2014) A fully traits-based approach to modeling  
842 global vegetation distribution. *Proceedings of the National Academy of Sciences*, **111**, 13733-  
843 13738.
- 844 Van Der Plas F, Manning P, Allan E *et al.* (2016) Jack-of-all-trades effects drive biodiversity-  
845 ecosystem multifunctionality relationships in European forests. *Nat Commun*, **7**, 11109.
- 846 Van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree  
847 mortality rates in a temperate forest. *Ecology Letters*, **10**, 909-916.
- 848 Vayreda J, Gracia M, Martínez-Vilalta J, Retana J (2013) Patterns and drivers of regeneration  
849 of tree species in forests of peninsular Spain. *Journal of Biogeography*, **40**, 1252-1265.
- 850 Vayreda J, Martínez-Vilalta J, Gracia M, Canadell JG, Retana J (2016) Anthropogenic-driven  
851 rapid shifts in tree distribution lead to increased dominance of broadleaf species. *Global*  
852 *Change Biology*, **22**, 3984-3995.
- 853 Vayreda J, Martínez-Vilalta J, Gracia M, Retana J (2012) Recent climate changes interact with  
854 stand structure and management to determine changes in tree carbon stocks in Spanish forests.  
855 *Global Change Biology*, **18**, 1028-1041.
- 856 Vicente-Serrano SM, Beguería S, López-Moreno JI, Angulo M, El Kenawy A (2010) A new  
857 global 0.5° gridded dataset (1901-2006) of a multiscalar drought index: Comparison with  
858 current drought index datasets based on the Palmer drought severity index. *Journal of*  
859 *Hydrometeorology*, **11**, 1033-1043.

- 860 Vilà-Cabrera A, Martínez-Vilalta J, Vayreda J, Retana J (2011) Structural and climatic  
861 determinants of demographic rates of Scots pine forests across the Iberian Peninsula.  
862 *Ecological Applications*, **31**, 1162-1172.
- 863 Violle C, Reich PB, Pacala SW, Enquist BJ, Kattge J (2014) The emergence and promise of  
864 functional biogeography. *Proceedings of the National Academy of Sciences*, **111**, 13690-  
865 13696.
- 866 Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*,  
867 **199**, 213-227.
- 868 Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies:  
869 some leading dimensions of variation between species. *Annual Review of Ecology and*  
870 *Systematics*, **33**, 125-159.
- 871 Wolf HP, Bielefeld U (2014) aplpack: Another Plot PACKage: stem.leaf, bagplot, faces,  
872 spin3R, plotsummary, plothulls, and some slider functions. pp Page.
- 873 Zavala MA, Espelta JM, Retana J (2000) Constraints and trade-offs in Mediterranean plant  
874 communities: The case of holm oak-aleppo pine forests. *Botanical Review*, **66**, 119-149.
- 875 Zavala MA, Zea E (2004) Mechanisms maintaining biodiversity in Mediterranean pine-oak  
876 forests: insights from a spatial simulation model. *Plant Ecology*, **171**, 197-207.
- 877 Zhang J, Huang S, He F (2015) Half-century evidence from western Canada shows forest  
878 dynamics are primarily driven by competition followed by climate. *Proceedings of the National*  
879 *Academy of Sciences*, **112**, 4009-4014.
- 880 Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in  
881 response to climate change. *Global Change Biology*, **18**, 1042-1052.
- 882 Zomer RJ, Trabucco A, Bossio DA, Verchot LV (2008) Climate change mitigation: A spatial  
883 analysis of global land suitability for clean development mechanism afforestation and  
884 reforestation. *Agriculture, Ecosystems & Environment*, **126**, 67-80.
- 885 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and*  
886 *extension in Ecology with R*, New York, USA, Springer.

## 887 **Supporting Information**

888 Additional Supporting Information may be found in the on-line version of this article:

889 **Appendix S1** Further details of the individual National Forest Inventories.

890 **Appendix S2** Detailed methods for the multilevel path analyses of functional changes across Europe.

891 **Appendix S3** Changes in functional composition in plots with no record of recent management.

892 **Appendix S4** Changes in the proportion of gymnosperms between consecutive inventories.

893 **Table S1** Trait data used in the study.

894 **Table S2** Estimated parameters and standard errors for the best models predicting changes in  
895 multidimensional functional space.

896 **Fig. S1** Map of positive, negative and no changes in functional composition for each forest type.

897 **Fig. S2** Histograms and density curves of the changes in functional composition for each functional  
898 trait and forest type.

899 **Fig. S3** Spatial distribution of the explanatory variables in the National Forest Inventories included in  
900 the study.

901 **Fig. S4** Results of the Principal Component Analysis of the standardised changes in functional  
902 composition.

903 **Fig. S5** Map of the first and second axis of the Principal Component Analyses performed with the  
904 functional traits.

905 **Fig. S6** Histograms of residuals and standard residuals versus fitted values for PC1 and PC2 best models

906 **Fig. S7** Partial residual plots of explanatory variable for PC1 and PC2 final models.

907 **Fig. S8** Density plots of the NFI data along climatic and stand development variables.

908 **Fig. S9** Interactive effects of climatic and structural variables on the PC1, with colours relative to each  
909 forest type.

910 **Fig. S10** Maximum tree height for main species in each forest type.

911 **Table 1.** Functional traits used in this study, including their units, interpretation for ecosystem functioning and hypotheses that may explain  
 912 potential changes in forest composition. Also included whether the trait represents functional strategies that contrast between angiosperms (ANG)  
 913 and gymnosperm (GYM, based on Figure S1).

Trait	Functional interpretation of links to effects on Ecosystem Functions	Mechanisms leading changes*	ANG	GYM
Leaf mass per area (LMA, g m <sup>2</sup> )	Absorption (light, nutrients) Primary productivity Herbivory	Competition ability and forest succession (growth less sensitive to competition in angiosperms: trade-off between carbon gain and longevity)	Low	High
Wood density (WD, g cm <sup>-3</sup> )	Cell anatomy and resistance	Eco-physiological and hydraulic (angiosperms have higher capacity to reverse embolisms: trade-off between growth potential and embolism risk)	High	Low
Seed mass (SM, mg)	Dispersal, fecundity Response to disturbance	Life strategy (different strategies: trade-off between seedling survival versus colonization ability)	Low to high	Low
Water potential causing 50% loss of hydraulic conductivity ( $\psi_{50}$ , kpa)	Embolism resistance	Eco-physiological and hydraulic (angiosperms have narrower hydraulic safety margins)	High	Low
Maximum tree height (MTH, cm)	Light interception Primary productivity Response to disturbance	Competition ability (larger maximum tree height correlates with larger competitive abilities and successional progress)	*	*

914 Key references used: (Westoby, 1998, Chapin, 2003, Díaz *et al.*, 2004, Moles *et al.*, 2009, Choat *et al.*, 2012, Carnicer *et al.*, 2013, Reich, 2014,  
 915 Díaz *et al.*, 2016).

916 (\*) No strong differences between angiosperms and gymnosperms were found (see Appendix S4).

917 **Table 2** Comparisons of alternate models based on Akaike Information Criterion (AIC)  
 918 to test pair-wise interactions and main effects supported for the first and second axes (i.e.  
 919 PC1 and PC2) of the Principal Component Analysis of the absolute change in leaf mass  
 920 per area, seed mass, wood density, maximum tree height and water potential causing 50%  
 921 loss of hydraulic conductivity. Relative importance of variables was also tested using  
 922 Akaike weights for PC1 and PC2 ( $w_{PC1}$  and  $w_{PC2}$ , respectively).

(a) Testing interactions	$\Delta AIC_{PC1}$	$\Delta AIC_{PC2}$	(b) Testing main effects	$\Delta AIC_{PC1}$	$\Delta AIC_{PC2}$	Variables	$w_{PC1}$	$w_{PC2}$
Full	<b>0</b>	<b>0</b>	<b>Full</b>	<b>0</b>	<b>0</b>			
No WAI × TD	9	13	No ID	89	172	ID	1.00	1.00
No TA × TD	21	18	No dm	382	434	dm	1.00	1.00
No ID × TD	2	19	No WAI	486	1495	WAI	1.00	1.00
No WAI × d <sub>m</sub>	32	91	No TA	589	240	TA	1.00	1.00
No TA × d <sub>m</sub>	64	16	No TD	802	113	TD	1.00	1.00
No ID × d <sub>m</sub>	34	68	No FD	952	1619	FD	1.00	1.00
No WAI × FD	148	510	AIC	230286	174982			
No TA × FD	385	49	R <sup>2</sup>	10.82	10.76			
No ID × FD	80	33						
No ID × WAI	22	9						
No WAI × TA	50	5						
No TA × ID	71	24						

923 Comparisons of alternate models of changes of functional composition (i.e. PC1 and PC2)  
 924 based on Akaike Information Criterion (AIC) to test the support for (a) interactions, and  
 925 (b) main effects. The full models include the effects of water availability (WAI),  
 926 temperature anomaly (TA), intense drought (ID), tree density (TD), mean d.b.h. (d<sub>m</sub>) and  
 927 functional diversity (FD), and (a) all interactions tested, and (b) all interactions supported  
 928 by the best model in (a). The best fitting model (the full model in our case) is given a  
 929  $\Delta AIC$  value of zero (bold). This model is compared with models in which the effect of  
 930 the individual predictor variables (considering the main effects and/or the interactions)  
 931 has been removed. Thus, the alternate models ignore the effects ('No') of (a) interactions;  
 932 and (b) main effects of the predictor variables and the interactions where the variable is

933 involved. The AIC for the best models and the pseudo R<sup>2</sup> for the best models are also  
934 shown.



935 **FIGURE LEGENDS**

936

937 **Figure 1.** First and second axis of a Principal Component Analysis showing National  
938 Forest Inventory plots (grey circles) and changes in functional composition for each  
939 functional trait (arrows), including: LMA (change in leaf mass per area,  $\text{g m}^{-2}$ ), WD  
940 (change in wood density,  $\text{g cm}^{-3}$ ), SM (change in seed mass, mg), P50 (change in water  
941 potential causing 50% loss of hydraulic conductivity, MPa), and MTH (change in  
942 maximum tree height, m).

943

944 **Figure 2.** Graphical representation of the effects of climate (i.e. abiotic factors, orange  
945 box), stand development (i.e. biotic factors, green box) and demographic rates (blue box)  
946 on changes in functional composition (represented by black arrows). See Figure S6 for a  
947 detailed description of acyclic graph.

948

949 **Figure 3.** Interactive effects of climatic and structural variables on the first axis of the  
950 PCA (PC1) in each forest type studied: (a) broad-leaved deciduous, (b) broad-leaved  
951 evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen Mediterranean  
952 forests. Blue colour represents positive values in the PC1 indicating changes towards  
953 lower LMA and higher WD, while red colour represents changes towards lower WD and  
954 higher LMA. The variables vary between the observed 99% percentiles in each forest  
955 type. Convex hull lines covering the presence of data points in each panel are represented  
956 using black lines and density plots are shown in Fig. S8.

957 Climatic and structural variables include: water availability (WAI, %), temperature  
958 anomaly (TA, °C), drought intensity (Drought, more negative values of SPEI mean more

959 intense droughts, adimensional), tree density (Density, No. trees/ha), mean tree diameter  
 960 (Size, mm) and functional diversity (Diversity, adimensional).

961

962 **Figure 4.** Interactive effects between climatic and structural variables on the second axis  
 963 of the PCA (PC2) in each forest type studied: (a) broad-leaved deciduous, (b) broad-  
 964 leaved evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen  
 965 Mediterranean forests. Green colour represents positive values in the PC2 indicating  
 966 changes towards higher maximum tree heights, while brown colour represents the  
 967 opposite. The variables vary between the observed 99% percentiles in each forest type.  
 968 Convex hull lines covering the presence of data points in each panel are represented using  
 969 black lines and density plots are shown in Fig. S8.

970 Climatic and structural variables include: water availability (WAI, %), temperature  
 971 anomaly (TA, °C), drought intensity (Drought, more negative values of SPEI mean more  
 972 intense droughts, adimensional), tree density (Density, No. trees/ha), mean tree diameter  
 973 (Size, mm) and functional diversity (Diversity, adimensional).

974

975 **Figure 5.** Piecewise structural equation models exploring the direct effects of mortality  
 976 and growth on changes in functional composition (i.e. PC1 and PC2). Black boxes  
 977 represent measured variables and grey rectangles categories. Lines indicate the supported  
 978 causal relationships (i.e.  $P \geq 0.05$  of the estimated parameter in Appendix S2). The  
 979 estimated coefficient for the effects of mortality and growth is provided next to the arrow  
 980 and the thickness of the significant paths has been scaled based on the magnitude of the  
 981 standardised regression coefficient. The conditional  $R^2$  of the models (i.e. based on the  
 982 variance of both the fixed and random effects) is provided in in the boxes of response  
 983 variables.