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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 21st 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 m² ha⁻¹ 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⁻²), wood density (WD, g cm⁻³), 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 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⁻¹), 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⁻¹), and functional diversity; (ii) demography, i.e.
289 tree growth (log, cm² ha⁻¹ yr⁻¹) and tree mortality (log +0.01, cm² ha⁻¹ yr⁻¹), 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 R² (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 Δ 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⁻¹ 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⁻¹,
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⁻¹ 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⁻¹ 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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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 ²)	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 ⁻³)	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 (ψ_{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	ΔAIC_{PC1}	ΔAIC_{PC2}	(b) Testing main effects	ΔAIC_{PC1}	ΔAIC_{PC2}	Variables	w_{PC1}	w_{PC2}
Full	0	0	Full	0	0			
No WAI \times TD	9	13	No ID	89	172	ID	1.00	1.00
No TA \times TD	21	18	No dm	382	434	dm	1.00	1.00
No ID \times TD	2	19	No WAI	486	1495	WAI	1.00	1.00
No WAI \times d _m	32	91	No TA	589	240	TA	1.00	1.00
No TA \times d _m	64	16	No TD	802	113	TD	1.00	1.00
No ID \times d _m	34	68	No FD	952	1619	FD	1.00	1.00
No WAI \times FD	148	510	AIC	230286	174982			
No TA \times FD	385	49	R ²	10.82	10.76			
No ID \times FD	80	33						
No ID \times WAI	22	9						
No WAI \times TA	50	5						
No TA \times 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_m) 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 ΔAIC 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 R² 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, g m^{-2}), WD
940 (change in wood density, 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.