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Tree mortality drives recent changes in functional composition across European forests

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Abstract:	Intense droughts combined with increased temperatures are one of the major threats to forest persistence in the 21st century. Despite the direct impact of climate change on forest growth and shifts in species abundance, the effect of altered demography on changes in the composition of functional traits is not well known. We sought to: (1) quantify the changes in functional composition of European forests; (2) identify the relative importance of climate change, mean climate and forest development for changes in functional composition; and (3) analyse the roles of tree mortality and growth underlying any functional changes in different forest types. We quantified changes in functional composition from the 1980s to the 2000s across Europe by two dimensions of functional trait variation: the first dimension was mainly related to changes in leaf mass per area

and wood density (i.e. angiosperm vs. gymnosperm dichotomy), and the second dimension related to changes in maximum tree height. Our results indicate that climate change and mean climatic effects strongly interacted with forest development and it was not possible to completely disentangle their effects. Where recent climate change was not too extreme the patterns of functional change generally followed the expected patterns under secondary succession (e.g. larger proportion gymnosperms in forest widely distributed in Europe and changes towards higher maximum tree heights) and latitudinal gradients (e.g. larger proportion of gymnosperm strategies at low water availability in broad-leaved deciduous forests). Recent climate change favoured the dominance of angiosperms under increased temperature and, under intense droughts generally resulted in a major dominance of a functional strategy different from the dominant one. Our results show substantial changes in functional composition over relatively short time scales in European forests, and indicate the key role of tree mortality, which should be further investigated to adequately predict the impacts of climate change.

Tree mortality drives recent changes in functional composition across European forests

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Running head: Functional composition changes in forests

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Abstract

Intense droughts combined with increased temperatures are one of the major threats to forest persistence in the 21st century. Despite the direct impact of climate change on forest growth and shifts in species abundance, the effect of altered demography on changes in the composition of functional traits is not well known. We sought to: (1) quantify the changes in functional composition of European forests; (2) identify the relative importance of climate change, mean climate and forest development for changes in functional composition; and (3) analyse the roles of tree mortality and growth underlying any functional changes in different forest types. We quantified changes in functional composition from the 1980s to the 2000s across Europe by two dimensions of functional trait variation: the first dimension was mainly related to changes in leaf mass per area and wood density (i.e. angiosperm vs. gymnosperm dichotomy), and the second dimension related to changes in maximum tree height. Our results indicate that climate change and mean climatic effects strongly interacted with forest development and it was not possible to completely disentangle their effects. Where recent climate change was not too extreme the patterns of functional change generally followed the expected patterns under secondary succession (e.g. larger proportion gymnosperms in forest widely distributed in Europe and changes towards higher maximum tree heights) and latitudinal gradients (e.g. larger proportion of gymnosperm strategies at low water availability in broad-leaved deciduous forests). Recent climate change favoured the dominance of angiosperms under increased temperature and, under intense droughts generally resulted in a major dominance of a functional strategy different from the dominant one. Our results show substantial changes in functional composition over relatively short time scales in European forests, and indicate the key role of tree mortality, which should be further investigated to adequately predict the impacts of climate change.

Introduction

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

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

The effect of climate change on forest species composition and functioning might depend on the functional traits of the dominant species (e.g. Jucker *et al.*, 2014, Ratcliffe *et al.*, 2016, Ruiz-Benito *et al.*, 2016), legacy effects (e.g. past management, disturbance and previous extreme droughts; Bengtsson *et al.*, 2000, Anderegg *et al.*, 2015, Clark *et al.*, 2016, Perring *et al.*, 2016), and forest succession and development (e.g. Ruiz-Benito *et al.*, 2013, García-Valdés *et al.*, 2015). Co-variation and trade-offs between traits implies that functional strategies can be summarized using a few axes of trait variation (Westoby, 1998, Westoby *et al.*, 2002). The axes of variation generally correspond well to angiosperm vs. gymnosperm strategies, which also have many contrasting functional traits that can be linked to the individual response to environmental conditions (Brodribb *et al.*, 2012, Carnicer *et al.*, 2013). It has been suggested that gymnosperms have a greater ability to withstand abiotic stress (i.e. high persistence) while angiosperms have a greater competitive ability and tend to dominate in diverse forests (Coomes *et al.*, 2005, Carnicer *et al.*, 2013). Despite the current evidence from regional to global scales of increased tree mortality due to higher temperatures and intense droughts (Anderegg *et al.*, 2013), little is known about the actual impact of climate change on changes in forest functional trait composition. The use of functional traits is emerging as a promising approach to study the impacts of climate change on ecosystem functioning (Suding *et al.*, 2008, Violle *et al.*, 2014), because alterations in the dominance of key functional traits can be directly linked to changes in ecosystem functioning (see Table 1).

Here, we quantified recent changes in forest functional composition through changes in the dominance of five key functional traits using resurveyed data from *c.* 68,000 permanent forest plots including 143 species spanning Mediterranean to temperate and boreal climates. Our objectives were to: (1) quantify the main temporal changes in functional composition of

European forests; (2) identify the relative importance of climate change, mean climate and forest development; and (3) disentangle the roles of tree mortality and growth underlying any changes in different forest types. To our knowledge, these analyses for the first time link large-scale spatial changes in forest functional composition with recent temporal changes in climate, revealing critical information for predicting future changes in species composition and forest ecosystem function.

Materials and methods

Inventory platform and study area

We compiled data from the National Forest Inventories (NFIs) of Finland, Germany, Spain, Sweden and Wallonia (Belgium) (see a detailed description in Appendix S1 and Table S1) covering the large latitudinal gradient of Europe (*c.* 5.000 km). For each tree we compiled information on the species identity (see Table S2), d.b.h. and status (alive or dead). To select comparable data from the inventories we only included re-surveyed plots with a basal area equal or greater than 4 m^2 ha^{-1} and trees with a minimum d.b.h. of 10 cm in the consecutive surveys; and we only included plots where the time between surveys was equal to or larger than 5 years (mean = 11.32).

European forests cover a large latitudinal and climatic gradient extending from boreal to temperate and Mediterranean climates (Fig. 1). We classified each plot according to (i) the abundance of the species depending on leaf type and habit (i.e. broad- vs. needle-leaved, deciduous vs. evergreen), and (ii) the Mediterranean character of the species (i.e. some species are restricted to Mediterranean climates, while others distribute from boreal to temperate and Sub-Mediterranean biomes, see Table 1). We used this classification because we expected angiosperm and gymnosperm forests to have different responses to drought and increased temperature (Brodribb *et al.*, 2012, Carnicer *et al.*, 2013) and the response to climate may be different in forests well adapted to limited water availability (e.g. Grossiord *et al.*, 2014). From the *c.* 68,000 permanent plots, we only considered forest types with more than 1,000 plots: broad-leaved deciduous (15,234 plots), needle-leaved evergreen (32,215 plots), needle-leaved evergreen Mediterranean (9,395 plots) and broad-leaved evergreen Mediterranean forests (5,550 plots, Fig. 1).

Patterns of change in functional composition across European forests

Functional composition was calculated as the community-level weighted means (i.e. mean value of each trait in each plot weighted by the relative abundance of each species in basal area terms; Lavorel *et al.*, 2008). We used five traits: leaf mass per area (LMA, g m^{-2}), wood density (WD, g cm^{-3}), seed mass (SM, mg), water potential causing 50% loss of hydraulic conductivity (P50, MPa), and maximum tree height (MTH, m). Trait information was compiled via the TRY Initiative (http://www.try-db.org; Kattge *et al.*, 2011) and additional references (Table S2). We quantified changes in functional composition as the absolute annual change in each functional trait selected instead of a relative change, because it informs about the direction of the change and its magnitude (i.e. positive or negative, and the absolute value of the change, Fig. 1 and Fig. S2). There were strong correlations in the absolute changes in different functional traits (Fig. S3) and, thus, we explored the relationship between the response variables using a Principal Component Analyses (R Development Core, 2014). We used the first two axes of the PCA as representative of the changes in functional composition; as between them they explained 70% of the variation in the functional changes.

Potential drivers of changes in forest functional composition

Each forest inventory plot was characterised by climate, stand development and demographic rate variables (see Fig. S1). Climate was defined by variables related to a selection of its components: (i) *mean climate*: potential evapotranspiration (PET, mm), aridity (i.e. PET/annual precipitation, adimensional), and water availability (i.e. (annual precipitation – PET)/PET, %), downloaded from CGIAR-CSI GeoPortal (Zomer *et al.*, 2008); (ii) *recent* *changes in mean climate*: temperature and precipitation anomaly, defined as the difference between the mean temperature or precipitation for the study period (i.e. years between the two consecutive inventories plus two years before the first survey) and the mean value for the reference period (1900-2010) in each of the NFI plots (UDel_AirT_Precip data, Boulder, Colorado, USA); and (iii) *recent climate change due to drought events*: mean SPEI (mean standardised precipitation-evapotranspiration index value for the period between the inventory surveys, adimensional), frequency of dry years (i.e. years between the consecutive inventories with SPEI < 0, No. of years), and the most intense drought (a dimension less index calculated as the lowest SPEI value between the consecutive inventories); calculated from SPEIbase v2.2. (Vicente-Serrano *et al.*, 2010). From this list of variables we selected variables representative of each aspect that were not strongly correlated and had low Variance Inflation Factor (i.e. $r < 0.6$ and VIF < 4, see Dormann *et al.*, 2013): (i) water availability (WAI, %), (ii) temperature anomaly (TA, C), and (iii) the most intense drought (ID, adimensional)

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

Statistical analysis

The importance of climate, stand development and demography on changes in functional composition were assessed using three steps. Firstly, we evaluated changes in functional composition of European forests as described above. Secondly, we identified the climatic and forest developmental drivers of changes in functional composition using linear mixed-effect models. Thirdly, we quantified the effect of demographic rates on changes in functional composition using piecewise structural equation models.

Patterns of change in functional composition depending on climate and forest development

We modelled absolute changes in functional composition (PC1 and PC2 axes) using linear mixed-effects models with a normal distribution of residuals. Due to the hierarchical nature of the sampling (where plots are aggregated in clusters for some countries; see Appendix S1 for more information), we included cluster identity nested in country as a random effect in the model to account for the lack of independence between the plots.

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

The most parsimonious model was determined using AIC (Akaike Information Criterion) as an indicator of both parsimony and likelihood (Burnham & Anderson, 2002). To identify the best-supported model, we first constructed candidate models in which each of the interactions were dropped. If the difference in AIC between the reduced and full models was less than two then the simpler model was selected, because it indicates substantial support for the model selected (Hilborn & Mangel, 1997, Burnham & Anderson, 2002). The process was then repeated for all the independent variables, each time comparing one individual predictor variable with a model containing all response variables without any interactions, using the differences in AIC to quantify the relative importance of each predictor variable. Finally, parameter estimates and confidence intervals of the best-supported model were obtained using restricted maximum likelihood (REML), which minimises the likelihood of the residuals from the fixed-effect portions of the model (Zuur *et al.*, 2009). Pseudo-R2 (proportion of variance explained by both the fixed and random factors) was used to provide an estimation of variance explained by fixed and random terms (Nakagawa & Schielzeth, 2013).

The predicted changes in functional composition for each forest type and explanatory variable (varying between the observed 99% percentiles) were computed using the best-supported model, fixing the values of the other continuous variables at their observed mean

(Table 1). These three dimensional predicted changes were visualised using heat graphs and the actual occurrence of the change in the NFI data for each forest types was indicated by black lines as a convex hull using aplpack library (Wolf & Bielefeld, 2014). All linear mixed effect models were fitted using lme4 library (Bates *et al.*, 2015) in R version 3.2.2. (R Core Team, 2015).

Changes in functional composition due to mortality and growth

We conducted piecewise structural equation modelling (Shipley, 2009) to test the relative importance of tree mortality and growth rates on changes in functional composition and to understand how patterns varied between the forest types, while accounting for the interactive effects of climate and stand development (see hypotheses in Fig. 2 and Fig. S4). The predictors included the exogenous variables (i.e. whose variance arose from outside the model) related to climate (water availability, temperature anomaly and intense droughts) and stand development (density, mean d.b.h. and functional diversity). We considered as endogenous variables (i.e. those whose variation the model seeks to explain): (i) demography, i.e. tree growth (log, m^2 ha^{-1} yr^{-1}) and tree mortality (log +0.01, m^2 ha^{-1} yr^{-1}), because it has been demonstrated that they both depend on climate and stand development; and (ii) changes in functional composition quantified as the first two PCA axes of the changes in the five functional traits.

The confirmatory multilevel path analysis was constructed to test the effects of demography on changes in functional composition, while accounting for climate and stand development, using the acyclic causal graphs (see Fig. S4). The model was evaluated using d-sep method, where the validity of each path model is tested by deriving a set of independence claims from each graph (Shipley, 2009). Using the mixed effects models (i.e. when applicable the random effect of country and cluster identity was included), the probabilities p_i of each of the k independent claims are obtained, which are then combined into the Fisher's C statistic:

$$C = -2\sum_{i=1}^{k} ln(p_i)$$

which follows a chi-squared distribution with $2k$ degrees of freedom (where k is equal the number of pairs in the basis set). Fisher's C statistic was used to obtain a value of Akaike's Information Criterion (AIC) as: AIC = C + 2K, where K is the likelihood degrees of freedom (i.e. total number of free parameters, see Shipley, 2013).

A multilevel path analysis was first performed for the entire dataset, including all the forest types, which allowed us to detect general trends in the changes in functional composition related to demography, climate, stand structure and diversity. Pseudo-R2 (proportion of variance explained by both the fixed and random factors) was used to provide an estimation of variance explained by fixed and random terms (Nakagawa & Schielzeth, 2013). The analysis was repeated on each forest type separately (i.e. one model per forest type) to identify any forest type-specific trends. All analyses were conducted in R using the piecewiseSEM library (Lefcheck, 2015) in R 3.2.0. (R Core Team, 2015).

Results

Recent patterns of change in functional composition across European forests

We analysed absolute changes in the CWMs of five functional traits. Our exploratory analysis indicated shifts to both positive and negative values for all five traits (i.e. both smaller and larger CWM values, Fig. S2) but we did not observe any clear spatial pattern of change (Fig. S5). The results of the PCA performed with the five functional traits showed that the first axis (explaining 50% of the variance) was strongly and negatively correlated to changes in LMA and positively correlated to changes in WD, P50 and SM (Fig. 3 and Fig. S3). These functional traits are strongly associated with functional strategies that distinguish between angiosperms and gymnosperms: positive values of PC1 reflect a greater dominance of angiosperm strategies, whereas negative values reflect a greater dominance of gymnosperm strategies (see Fig. S6). The second axis of the PCA (explaining 20% of the variance) was highly and negatively correlated with changes in MTH (Fig. 3 and Fig. S3). The second axis of the PCA relates to the differential competitive ability of species and successional status (Table 1). We selected the first and second axes of the PCA for our modelling approach (i.e. hereafter named PC1 and PC2) as representative of the major changes in forest functional composition across Europe.

The interactive effect of climate and forest development drives recent changes in forest functional composition

Full models of changes in functional composition based on PC1 and PC2 included all predictor variables for each forest type (see Table 2, model residuals in Fig. S7 and Fig. S8 and standardised parameter values in Table S4). Our results indicate interactive effects of climate and forest development on changes in functional composition, particularly between climate and functional diversity (i.e. both for PC1 and PC2, Table 2). In models predicting PC1 (i.e. different functional strategies), the inclusion of variables related to recent climate change was supported, but its importance was lower than for forest development (see drop in ΔAIC in Table 2 when temperature anomalies and intense droughts were dropped). In models predicting PC2, functional diversity and water availability were the most strongly supported variables (Table 2).

Figures 4 and 5 represent the predicted changes in functional composition measured through the PC1 and PC2 axis, respectively, for each forest type (see density plots in Fig. S9 and relative changes in PC1 in Fig. S10). The graphics have been coloured to reflect the direction of the change along the PCA axes. PC1 is related to shifts in functional trait values towards a higher proportion of angiosperm (blue colour in Fig. 4 means positive changes in PC1) or gymnosperms (red colour in Fig. 4 means negative changes in PC1, Fig. S2). PC2 was related to changes in maximum tree height (brown colour in Fig. 5 means decreases in maximum tree height).

In broad-leaved deciduous forests greater shifts in functional strategy (i.e. larger dominance of gymnosperms, corresponding to red colours in Fig. 4a) occurred where low water availability co-occurred with medium-high tree density or mean d.b.h.; where low temperature anomalies co-occurred with low mean d.b.h.; and in plots with high functional diversity or under intense droughts. In needle-leaved evergreen forests the greatest shifts in functional strategy (i.e. higher proportion of angiosperms corresponding to blue colours in Fig. 4b) occurred where relatively mild droughts co-occurred with large trees; and in plots with low functional diversity. In the case of Mediterranean forests we found similar patterns for broad- and needle-leaved species. Changes towards a stronger dominance of angiosperm strategies in Mediterranean forests (i.e. blue colours in Fig. 4c,d) were observed at high water availability, high temperature anomalies, relatively mild droughts, high tree density and large mean tree sizes. The only clear difference between the two forest types was the interaction between water availability and tree density: Mediterranean broad-leaved forests tended to change towards larger proportions of gymnosperms at low water availability irrespective of tree density, whereas this pattern was not clear in Mediterranean coniferous forests.

PC2 was related to changes in maximum tree height (Fig. 3). The strongest interactions between climate and stand development on changes in PC2 occurred in Mediterranean conifers followed by broad-leaved deciduous forests (Fig. 5). In Mediterranean conifers most of the changes were towards increases in MTH (i.e. negative values of PC2), especially at high functional diversity and medium to high mean tree density and d.b.h., and under intense droughts (Fig. 5d). The same patterns of change towards greater MTH were observed in broad-leaved deciduous forests, except in areas with high water availability and temperature anomaly (Fig. 5c).

Mortality and growth effects on recent changes in functional composition

Overall, tree mortality had a larger effect on changes in functional composition than tree growth (i.e. PC1 and PC2, see standardised effect sizes in Fig. 6), but the variance explained by growth was greater than for mortality (R^2: 0.58, 0.41, respectively; see Fig. 6). The effect of mortality was particularly strong and positive on PC1, which reflected a general change towards strategies with lower leaf mass per area and higher wood density, seed mass and water potential loss (i.e. angiosperm strategies). For PC2 the mortality effect was negative and the magnitude was less strong, which reflected a weak decrease in maximum tree heights. Furthermore, we found that the sign of the relationship between mortality and growth on changes in functional composition was consistent for all the forest types studied (see sign of standardised parameters in Table S5). The strongest effect of mortality on PC1 and PC2 was found in Mediterranean conifers (see magnitude of standardised parameters in Table S5).

Discussion

Our results suggest that recent climate change –i.e. both increased temperature and intense droughts– are critical drivers of recent changes in the functional composition of European forests. Under climate change the functional changes analysed were not always in the expected direction of succession. Overall, the importance of the interaction between climate and forest development agrees with previous studies that identified similar strong interactions for tree growth (e.g. Gómez-Aparicio *et al.*, 2011, Ruiz-Benito *et al.*, 2015), tree mortality (e.g. Vilà-Cabrera *et al.*, 2011, Ruiz-Benito *et al.*, 2013), recruitment (e.g. Carnicer *et al.*, 2014, Zhang *et al.*, 2015) and total changes in basal area and carbon storage (Vayreda *et al.*, 2012, Ruiz-Benito *et al.*, 2014b). We found that the interactive nature of the drivers underlying changes in functional composition was due to differential tree demography (Clark *et al.*, 2014, Zhang *et al.*, 2015), and that it appears to critically depend on tree mortality rates (Allen *et al.*, 2015).

Here, we summarised the changes in functional composition through the variation in two-dimensional axes of change related to: (i) the functional strategies of the species, reflecting differences in a continuum of traits from high leaf mass per area and low wood densities to low leaf mass per area and high wood density; and (ii) maximum tree height. Overall, the two axes of variation are in line with the Leaf-Height-Seed scheme (Westoby, 1998), which captures variation in functional traits while considering the importance of stem density for woody plants (Chave *et al.*, 2009, Reich, 2014). These axes of variation reflect the two dominant strategies of gymnosperms and angiosperms (Stahl *et al.*, 2014) and correspond to the major trends of variation found in plant forms worldwide (Díaz *et al.*, 2016). The first axis (leaf mass – wood density) is a good predictor of resource use and responses to environmental conditions (Table 1). In turn it corresponds to a change towards a greater proportion of angiosperms or gymnosperms and, therefore, can be interpreted as changes in dominance of the angiosperm vs. gymnosperm functional strategy of each forest type. The second axis (maximum tree height) is strongly related to the differential competitive ability of the species and, therefore, to the successional progress of each forest stand (Table 1). Although changes in each functional trait can be highly informative we selected the PCA axes for an overall understanding of community-level functional changes, which is needed to further manage ecosystems and understand potential effects of climate change (see e.g. de Bello *et al.*, 2010).

Recent climate change impacts on recent changes in functional strategies across European forests

Recent climate change, via increases in temperature and intense droughts, is leading to directional changes across European forests, but these changes are also dependent on forest development. In relatively mature forests with large temperature anomalies we found a change towards a greater proportion of angiosperms in all forest types except conifer forests distributed across the entire latitudinal European gradient. Our observation that gymnosperms could be more vulnerable to increases in temperature and water stress agrees with recent studies that observed high mortality in conifers (McDowell *et al.*, 2016), and studies suggesting that warming could be promoting climatic conditions more favourable for angiosperms (e.g. Henne *et al.*, 2015, McIntyre *et al.*, 2015). However, we cannot discount the possibility that the observed functional changes towards a greater proportion of angiosperm strategies under increased temperature may be coupled to land-use changes promoting an increase in the relative abundance of oaks and other hardwoods (Carnicer *et al.*, 2014, Henne *et al.*, 2015, Vayreda *et al.*, 2016). Angiosperms have been favoured by relatively recent processes that affect secondary succession, such as agricultural abandonment and changes in management practices –e.g. coppicing, charcoal production– (Barberó *et al.*, 1998, Urbieta *et al.*, 2008, Müllerová *et al.*, 2015).

Functional changes towards a different strategy than the dominant one occurred under intense droughts in relatively mature forests of all forest types. However, this change was not observed in conifers of low-medium size (i.e. mean d.b.h. < 400 mm) and at low diversity (Fig. 4). The apparent shift in functional strategy is in accordance with previous studies that suggest trade-offs between plant size and drought tolerance (Ryan *et al.*, 2006, Moles *et al.*, 2009, Bennett *et al.*, 2015). The change towards traits linked to gymnosperm strategies in broad-leaved forests and small changes in conifer forests could be due to the highest mortality or lowest growth of the most dominant functional strategy in relatively mature forests, because all species are likely to be stressed if the drought is very extreme and water availability is too limiting (Choat *et al.*, 2012).

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

The recent changes in functional strategies (i.e. changes in PC1) across Europe were strongly dependent on the functional diversity and water availability of the forest stand, indicating that they mainly followed successional and biogeographical expectations. The influence of diversity was strong when compared to climatic variables, leading to clear patterns of change in all forest types, following the expected secondary succession patterns (Fig. 4). In Mediterranean forests we found greater shifts in the dominance of angiosperms in high diverse stands, whereas in forest distributed across the entire latitudinal gradient of Europe a greater dominance of gymnosperms and high diversity were linked. The trends observed at high diversity agree with the expectations of the secondary successional trajectory expected in the different forest types, which in Mediterranean forests generally leads to a greater dominance of late-successional hardwoods (Zavala & Zea, 2004, Carnicer *et al.*, 2014, Vayreda *et al.*, 2016). In contrast, forests distributed from temperate to boreal European biomes are generally changing towards a greater dominance of late-successional conifers (e.g. Angelstam & Kuuluvainen, 2004, Ratcliffe *et al.*, 2016). The change towards a greater dominance of gymnosperms at high diversity could also be due to the relatively higher growth rates of co-existing conifers when compared to slow-growing angiosperms, despite their lower competitive ability (e.g. Zavala *et al.*, 2000, Coomes *et al.*, 2005).

The observed shifts in functional strategies along the latitudinal gradient of Europe (i.e. delineated by water availability, Fig. S1a) agree with the expected biogeographical patterns of each forest type. Changes towards the most dominant functional trait values in each forest type occur where water is not too limiting (Fig. 4), which might imply that water availability is acting as a species filter at the continental scale (e.g. Šímová *et al.*, 2015). Firstly, in broad-leaved forests at low water availabilities we found the greatest change towards a greater dominance of gymnosperms, suggesting increased growth of fast-growing strategies (i.e. gymnosperms) and higher mortality of slow-growing strategies (i.e. angiosperms, Fig. 4a,b). At the rear edge of broadleaved forests (i.e. generally related to low water availability) an altered demography, where growth declines and mortality increases, could be driving the observed changes in functional strategies (Hampe & Petit, 2005, Jump *et al.*, 2006). Secondly, in conifers we found a larger transition towards angiosperm strategies at low water availability, which might be reflecting the expected altitudinal and latitudinal transition (Benito-Garzón *et al.*, 2013). Thirdly, in Mediterranean forests at high water availability we found shifts in functional composition towards a greater proportion of angiosperms, which agrees with observed recruitment trends along the Iberian Peninsula and it follows the expected advance of secondary succession (Vayreda *et al.*, 2013, Carnicer *et al.*, 2014, Vayreda *et al.*, 2016).

Most of the changes along climatic and forest development gradients were related to increases in maximum tree height (see Fig. 5). Functional diversity and water availability were the main drivers of the changes in maximum tree height, particularly in broad-leaved and Mediterranean coniferous forests. At high diversity we found generally an increase in maximum tree height, which might be reflecting the expected secondary succession trajectory (Marks *et al.*, 2016). In Mediterranean forests under intense droughts we found changes towards taller trees in more mature forests. This is congruent with the importance of maximum tree height for tree growth in the latitudinal extremes of Europe (Ratcliffe *et al.*, 2016) and the greater dominance of tall trees expected in warm sites not limited by water (Šímová *et al.*, 2015) (i.e. high water availability and no extreme temperature anomalies), particularly in mature forests. In areas where water is not limited we found that Mediterranean conifer forests (i.e. maximum height *c.* 28 m, see Fig. S11) tended to shift towards a higher dominance of tall species at high diversity, which agrees with the successional change expected towards broad-leaved deciduous species (e.g. *Fagus sylvatica*, *Quercus robur*, *Q. petraea* and *Castanea sativa*; maximum height *c.* 41 m, (Rivas-Martínez, 1987, Costa *et al.*, 1997). However, in areas of low water availability and mild drought changes towards shorter statured trees could be reflecting a transition towards Mediterranean and Sub-Mediterranean species (e.g. maximum height of *Q. ilex* and *Q. suber c.* 19 m; and *Q. faginea* and *Q. pyrenaica c.* 24 m, see Fig. S11). The transition between Mediterranean conifers and oaks is typical of the drier end of the water availability gradient, where a shifting mosaic between pines and oaks depends on management and landscape heterogeneity (Zavala *et al.*, 2000, Zavala & Zea, 2004), in agreement with the current and past co-dominance of these two groups in the Mediterranean from paleo-ecological data (Carrion *et al.*, 2001).

The role of demography underlying changes in functional composition

Our results suggest a critical role of tree mortality for changes in the functional composition of European forests undergoing secondary succession, which agrees with previous studies conducted from tropical to temperate and boreal forests (van Mantgem & Stephenson, 2007, Lasky *et al.*, 2014, Zhang *et al.*, 2015). We identified tree mortality as a key driver of three patterns of change in the functional strategies observed across European forests. (i) Increased mortality of conifer species due to rising temperatures could be driving changes towards a greater dominance of angiosperms across Europe, as predicted by McDowell *et al.* (2016) in southwest USA, and changes observed towards contrasting functional groups compared to the dominant species under intense droughts in mature forests (i.e. larger proportion of low wood density and high leaf mass per area in broad-leaved forests). (ii) Increased mortality of broadleaved species at the dry edge of temperate species broadly distributed across Europe (i.e. at low water availability) may be leading to a greater dominance of gymnosperms at the rear edge of broad-leaved deciduous forests, as for example those forests dominated by *Fagus sylvatica* or *Quercus robur* (Peñuelas *et al.*, 2013). (iii) The change towards a larger proportion of angiosperms in Mediterranean mature forests, not strongly limited by water availability, agrees with the greater role of mortality as compared to growth in forest undergoing secondary succession, and might be associated with recent changes in forest management across Europe. This change could be due to the fact that pioneer species (i.e. conifers generally characterised by low wood density and high leaf mass per area) tend to show the highest growth rates (Ratcliffe *et al.*, 2016) but also the highest mortality rates (Benito-Garzón *et al.*, 2013, Ruiz-Benito *et al.*, 2013, Reich, 2014), leading to changes towards a larger proportion of angiosperms, as expected in Mediterranean climates (Urbieta *et al.*, 2008, Henne *et al.*, 2015).

Conclusions and implications

Overall, we found that changes in forest functional composition are largely driven by a trait-based differentiation of leaf-wood and height axis of functional traits (Díaz *et al.*, 2016). We found that most climatic and forest developmental conditions lead to functional changes in accordance with forest successional pathways. However, we found that recent climate change –i.e. increased temperature and intense droughts– might lead to different pathways of changes in functional strategies than those expected only from succession. We concluded that increased tree mortality is driving changes in functional strategies and maximum tree height which is leading to quantifiable changes in the functional composition of European forests, despite our greater ability to explain growth than mortality (Fig. 6). Our study suggest that climatic and forest developmental interactions are critical to adequately predict forest responses under climate change (van Bodegom *et al.*, 2014). Further studies are critically needed to understand drivers of tree mortality and link plant functional traits to ecosystem functioning responses (Reichstein *et al.*, 2014, Funk *et al.*, 2016) and drought effects to secondary succession and stand development (Clark *et al.*, 2016).

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Supporting Information

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

Appendix S1 Further details of the individual National Forest Inventories.

Table S1 List of species present in the plots of the National Forest Inventories included in the study.

Table S2 Trait data used in the study.

Table S3 Estimated parameters and standard errors for the best models predicting changes in multidimensional functional space.

Table S4 Conditional independence test applied via d-sep method.

Table S5. Standardised regression coefficients of piecewise structural equation models.

Fig. S1 Spatial distribution of the explanatory variables in the National Forest Inventories included in the study.

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

Fig. S3 Results of the Principal Component Analysis of the standardised changes in functional composition.

Fig. S4 Acylic graph showing the schematic representation of variables included in piecewise SEM.

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

Fig. S6 Box-whisker plots of each of the functional traits for the species present in the European National Forest Inventories used for angiosperms and gymnosperms groups.

Fig. S7 Histograms of residuals and standard residuals versus fitted values for PC1 and PC2 best models

Fig. S8 Partial residual plots of explanatory variable for PC1 and PC2 final models.

Fig. S9 Density plots of the NFI data along climatic and stand development variables.

Fig. S10 Interactive effects of climatic and structural variables on the PC1, with colours relative to each forest type.

Fig. S11 Maximum tree height for main species in each forest type.

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

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, Díaz *et al.*, 2016).

(*) No strong differences between angiosperms and gymnosperms were found (Fig. S6).

Table 2 Comparisons of alternate models based on Akaike Information Criterion (AIC) to test main effects and pair-wise interactions supported for the first and second axes (i.e. PC1 and PC2) of the Principal Component Analysis of the absolute change in leaf mass per area, seed mass, wood density, maximum tree height and water potential causing 50% loss of hydraulic conductivity.

(a) Testing interactions	**ΔAIC_{PC1}**	**ΔAIC_{PC2}**	**(b) Testing main effects**	**ΔAIC_{PC1}**	**ΔAIC_{PC2}**
Full	0	0	**Full**	**0**	0
No WAI × TD	**9**	**13**	No WAI	486	1495
No TA × TD	**21**	**18**	No TA	589	240
No ID × TD	2	**19**	No ID	89	172
No WAI × d_m	**32**	**91**	No TD	802	113
No TA × d_m	**64**	**16**	No d_m	382	434
No ID × d_m	**34**	**68**	No FD	952	1619
No WAI × FD	**148**	**510**	AIC	230286	174982
No TA × FD	**385**	**49**	R^2	10.82	10.76
No ID × FD	**80**	**33**			
No ID × WAI	**22**	**9**			
No WAI × TA	**50**	**5**			
No TA × ID	**71**	**24**			

Comparisons of alternate models of changes of functional composition (i.e. PC1 and PC2) based on Akaike Information Criterion (AIC) to test the support for (a) interactions, and (b) main effects. The full models include the effects of water availability, temperature anomaly, intense drought, tree density, mean d.b.h. and functional diversity, and (a) all interactions tested, and (b) all interactions supported by the best model in (a). The best fitting model is given in ΔAIC value of zero (bold), comparing the full model with models dropping the effect of the predictor variables considering the main effects and/or the interactions. Thus, the alternate models ignore the effects ('No') of (a) interactions; and (b) main effects of the predictor variables and the interactions where the variable is involved. The AIC for the best models and the pseudo R^2 for the best models are also shown.

FIGURE LEGENDS

Figure 1. Map of forest types included in the analyses: broad-leaved deciduous, needle-leaved evergreen, needle-leaved evergreen Mediterranean and broad-leaved evergreen Mediterranean forests. The pie-chart indicates the percentage of plots showing some change between the consecutive surveys in any of the five functional traits considered (i.e. leaf mass per area, wood density, seed mass, water potential loss or maximum tree height). The absolute values (i.e. positive vs. negative change) are shown for leaf mass per area.

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

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

Figure 4. Interactive effects of climatic and structural variables on the first axis of the PCA (PC1) in each forest type studied: (a) broad-leaved deciduous, (b) broad-leaved evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen Mediterranean

forests. Blue colour represents positive values in the PC1 indicating changes towards higher proportion of angiosperm (i.e. lower LMA and higher WD, SM and P50), while red colour represents higher proportions of gymnosperms (i.e. lower WD, SM and P50 and higher LMA. Convex hull lines covering the presence of data points in each panel are represented using black lines and density plots are shown in Fig. S9.

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

Figure 5. Interactive effects between climatic and structural variables on the second axis of the PCA (PC2) in each forest type studied: (a) broad-leaved deciduous, (b) broad-leaved evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen Mediterranean forests. Green colour represents positive values in the PC2 indicating changes towards higher maximum tree heights, while brown colour represents the opposite. Convex hull lines covering the presence of data points in each panel are represented using black lines sand density plots are shown in Fig. S9.

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

Figure 6. Piecewise structural equation models exploring the direct effects of mortality and growth on changes in functional composition (i.e. PC1 and PC2). Black boxes represent measured variables and grey rectangles categories. Lines indicate the

supported causal relationships (i.e. P ≥ 0.05 of the estimated parameter in Table S5). The estimated coefficient for the effects of mortality and growth is provided next to the arrow. The thickness of the significant paths has been scaled based on the magnitude of the standardised regression coefficient. The conditional R^2 (i.e. based on the variance of both the fixed and random effects) is provided in in the boxes of response variables.

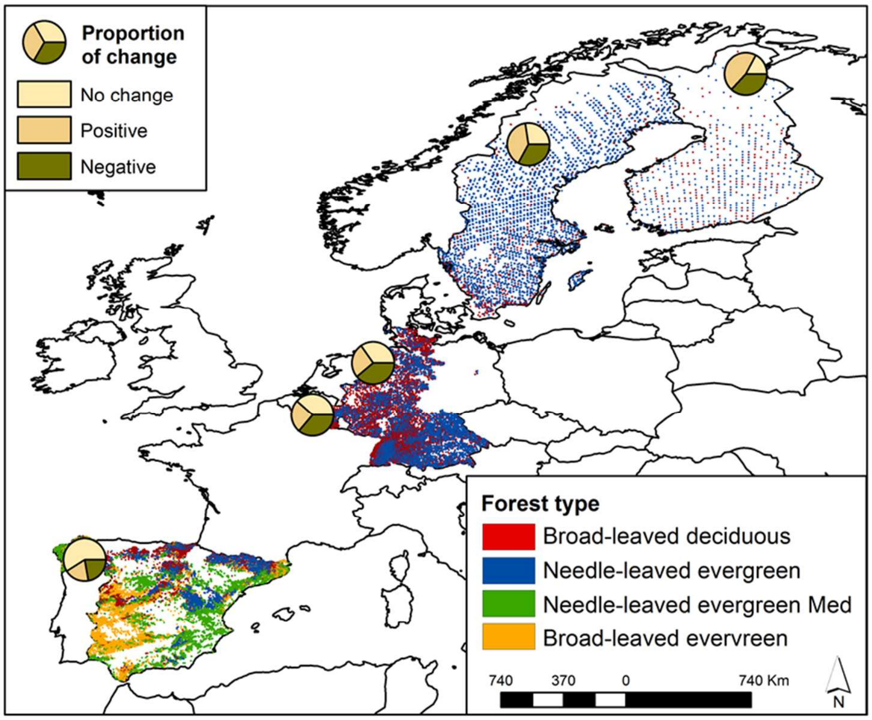
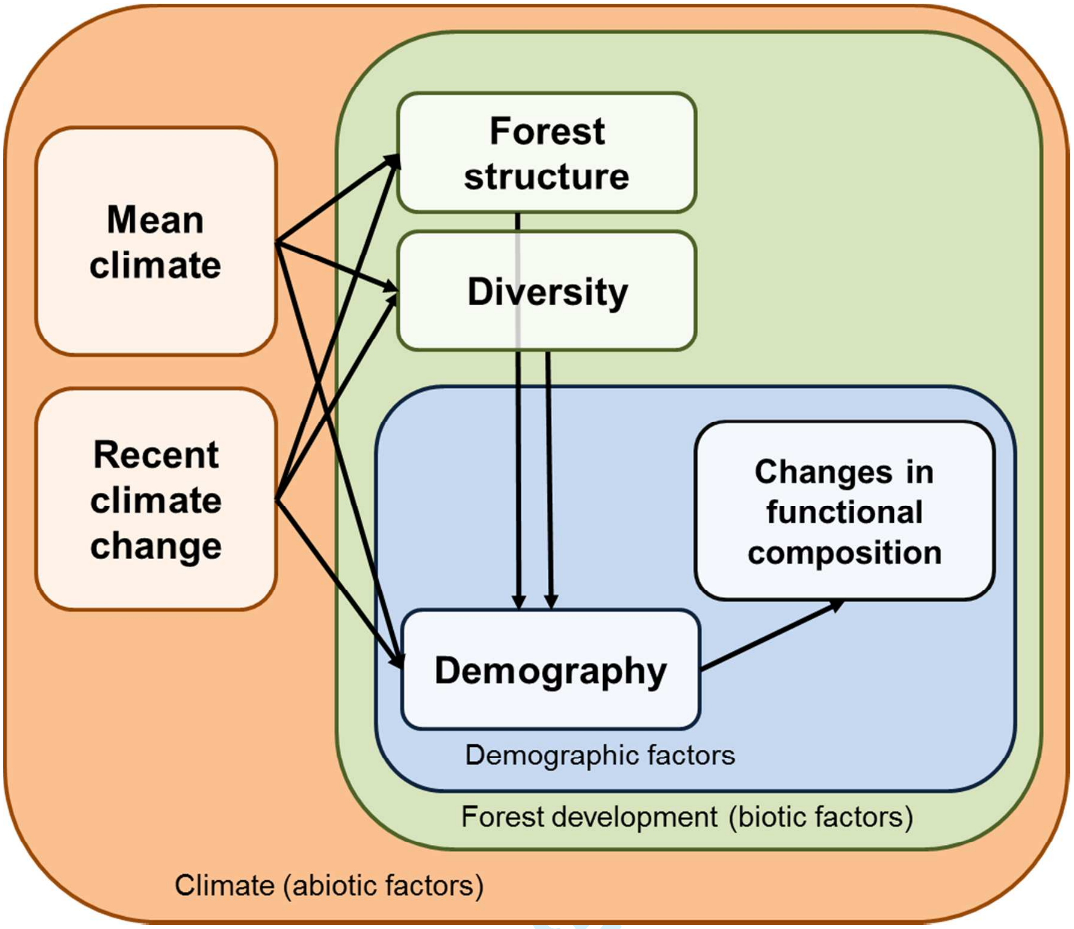
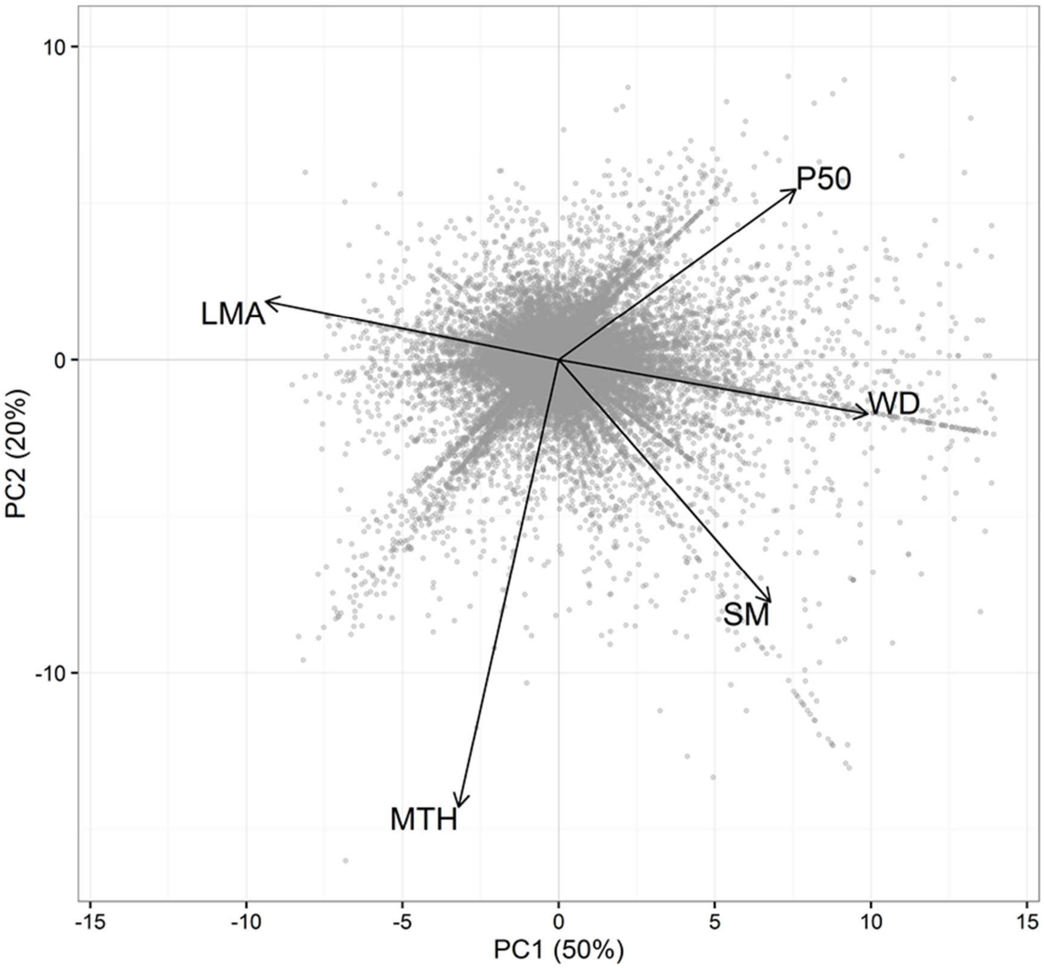

Proportion of change
No change
Positive
Negative
Forest type
Broad-leaved deciduous
Needle-leaved evergreen
Needle-leaved evergreen Med
Broad-leaved evervreen
740
370
0
740 Km
N

Figure 1.



911

912 **Figure 2.**



913

914 **Figure 3.**

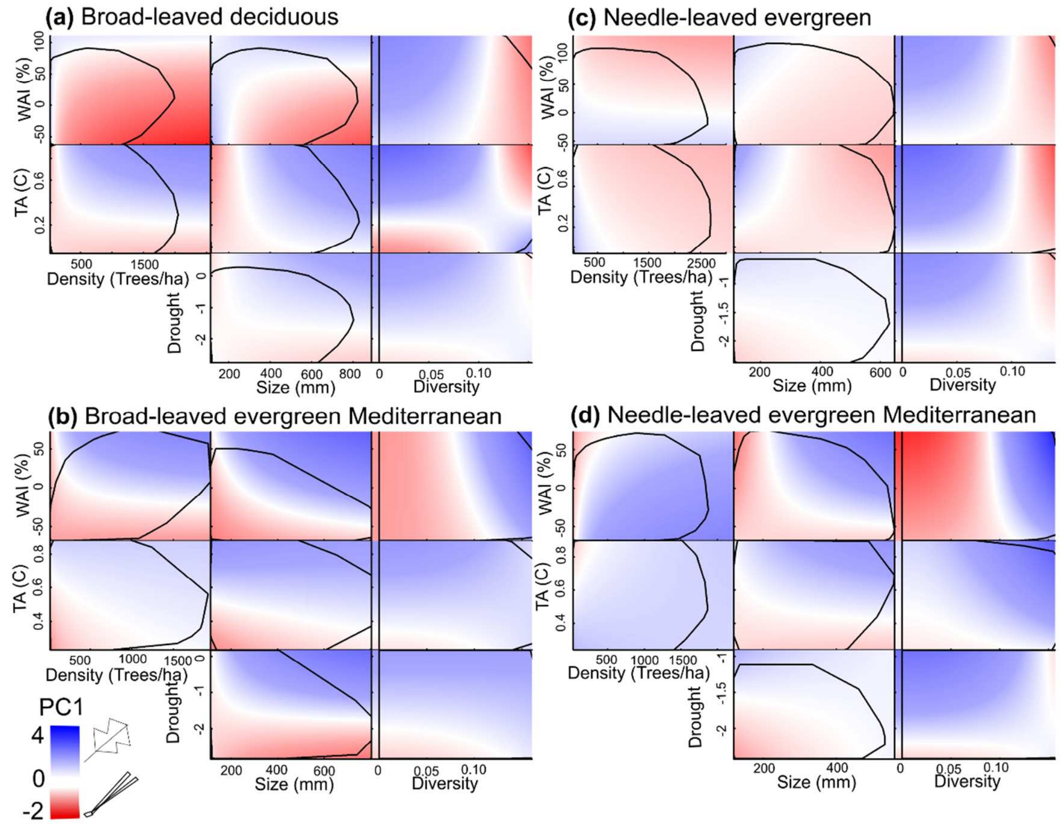

(a) Broad-leaved deciduous
(c) Needle-leaved evergreen
(b) Broad-leaved evergreen Mediterranean
(d) Needle-leaved evergreen Mediterranean
WAI (%)
TA (C)
Drought
Density (Trees/ha)
Size (mm)
Diversity
PC1
4
0
-2

Figure 4.

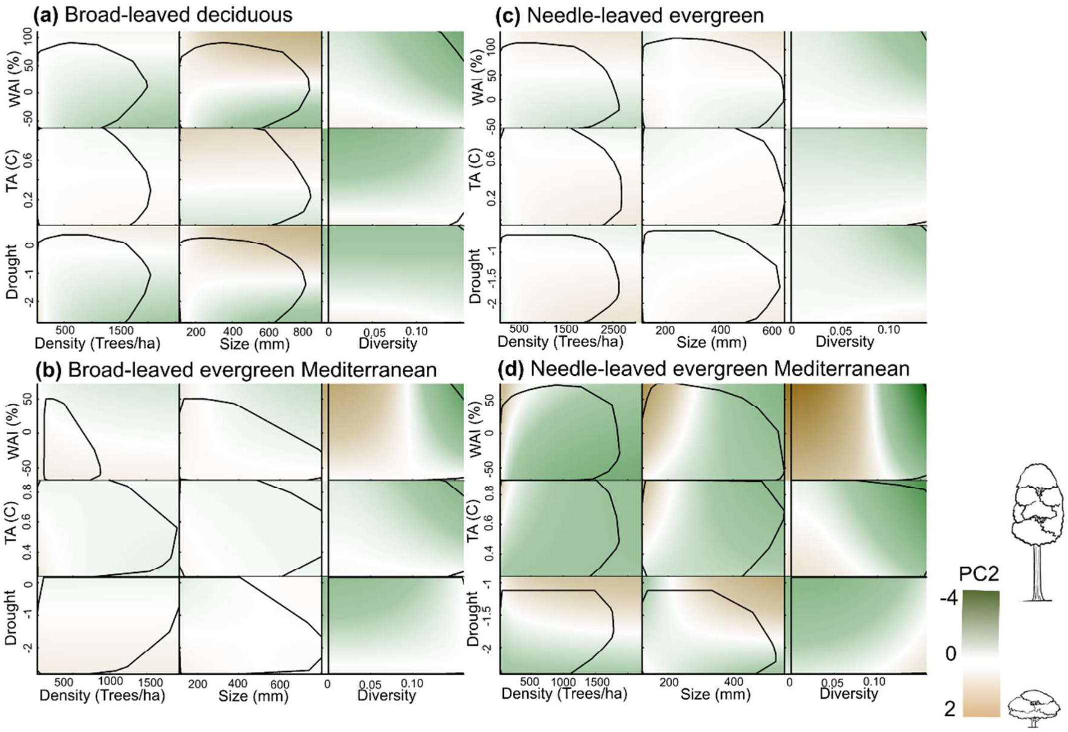
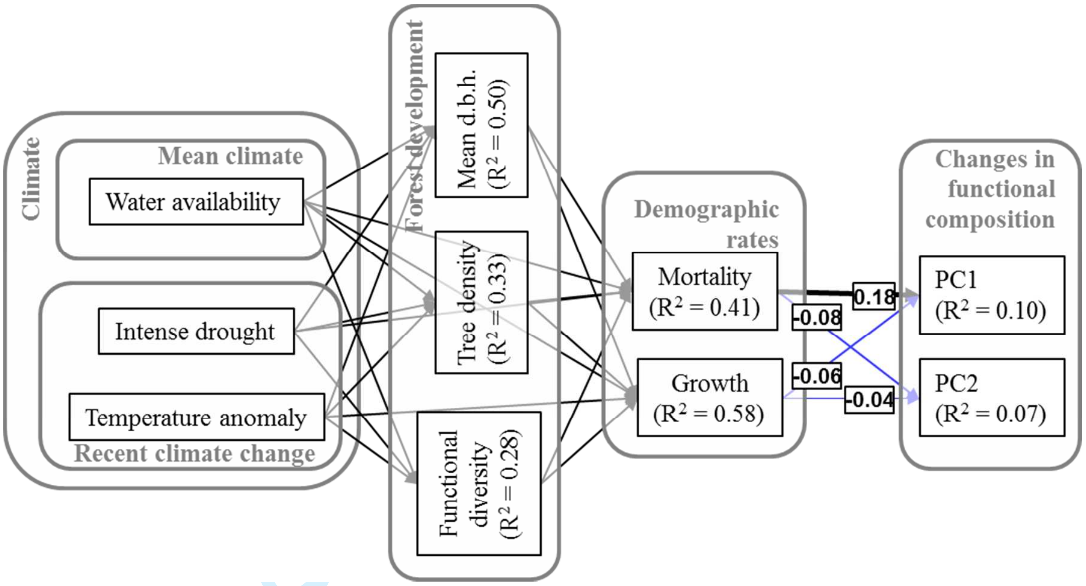

(a) Broad-leaved deciduous
WAI (%)
100
50
0
-50
TA (C)
0.6
0.2
Drought
0
-1
-2
500
1500
Density (Trees/ha)
200
400
600
800
Size (mm)
0
0.05
0.10
Diversity
(c) Needle-leaved evergreen
WAI (%)
100
50
0
-50
TA (C)
0.6
0.2
Drought
-1
-1.5
-2
500
1500
2500
Density (Trees/ha)
200
400
600
Size (mm)
0
0.05
0.10
Diversity
(b) Broad-leaved evergreen Mediterranean
WAI (%)
50
0
-50
TA (C)
0.8
0.6
0.4
Drought
0
-1
-2
500
1000
1500
Density (Trees/ha)
200
400
600
Size (mm)
0
0.05
0.10
Diversity
(d) Needle-leaved evergreen Mediterranean
WAI (%)
50
0
-50
TA (C)
0.8
0.6
0.4
Drought
-1
-1.5
-2
500
1000
1500
Density (Trees/ha)
200
400
Size (mm)
0
0.05
0.10
Diversity
PC2
-4
0
2

Figure 5.



920

921 **Figure 6.**

FOR ONLINE PUBLICATION ONLY

Ruiz-Benito P, Ratcliffe S, Zavala MA, Martínez-Vilalta J, Vila-Cabrera A, Lloret F, Madrigal-González J, Wirth C, Greenwood S, Kändler G, Lehtonen A, Kattge J, Dahlgren J, Jump AS. *Tree mortality drives recent changes in functional composition across European forests*. Global Change Biology

SUPPORTING INFORMATION

Appendix S1 Further details of the individual National Forest Inventories.

Table S1 List of species present in the plots of the National Forest Inventories included in the study.

Table S2 Trait data used in the study.

Table S3 Estimated parameters and standard errors for the best models predicting changes in multidimensional functional space.

Table S4 Conditional independence test applied via d-sep method.

Table S5. Standardised regression coefficients of piecewise structural equation models.

Fig. S1 Spatial distribution of the explanatory variables in the National Forest Inventories included in the study.

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

Fig. S3 Results of the Principal Component Analysis of the standardised changes in functional composition.

Fig. S4 Acylic graph showing the schematic representation of variables included in piecewise SEM.

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

Fig. S6 Box-whisker plots of each of the functional traits for the species present in the European National Forest Inventories used for angiosperms and gymnosperms groups.

Fig. S7 Histograms of residuals and standard residuals versus fitted values for PC1 and PC2 best models

Fig. S8 Partial residual plots of explanatory variable for PC1 and PC2 final models.

Fig. S9 Density plots of the NFI data along climatic and stand development variables.

Fig. S10 Interactive effects of climatic and structural variables on the PC1, with colours relative to each forest type.

Fig. S11 Maximum tree height for main species in each forest type.

Appendix S1. Further details regarding the National Forest Inventories used

Spanish National Forest Inventory: We used information from the second and third Spanish NFI (surveyed in the periods 1986-1996 and 1997-2007, respectively). The Spanish NFI plots are located on a 1 km^2 grid aver forested regions (Villaescusa & Díaz 1998; Villanueva 2004). Spanish NFI plots were sampled using a variable radius technique with four concentric circular subplots of radius 5, 10, 15 and 25 m. Within each subplot, trees were included in the sample according to their diameter at breast height (d.b.h.), with trees smaller than 12.4 cm measured in the 5 m radius subplot, those of 12.5-22.4 cm in the 10 m radius subplot, those of 22.5-42.4 cm in the 15 m radius subplot, and those with d.b.h. larger or equal to 42.5 cm in the 25 m radius subplot.

German National Forest Inventory: We used information from the first and second German NFI. The German NFI uses a systematic grid of clusters, sampled in the periods 1986-1990 (undertaken in West Germany only) and 2001-2002 respectively. The size of the sample grid is 4 by 4 km, however, it is reduced in some federal states to either 2.83 by 2.83 km or 2 by 2 km. Each cluster is a quadrangle of 150 m in length with a sample plot on each corner (Kändler 2009). Trees with a d.b.h. of 10 cm or more in the first inventory and 7 cm in the second were selected by the angle-count method with a basal area factor (BAF) of 4 m^2 ha^{-1} if they are alive or recently dead.

Wallonia National Forest Inventory (Belgium): The Wallonia NFI follows a systematic non-stratified sampling methodology on a 1 km by 0.5 km grid. One circular sampling plot is located within each grid intersection. Areas are sampled if the area of land is greater than 0.1 ha and has at least 10% covered by a forest canopy (trees must be able to reach a minimum of

5 m). Plots in the first census were surveyed between 1994 and 2003 and plots in the second census were surveyed between 2008 and 2011. The inventory employs a variable plot size depending on the circumference of the tree: trees from 70 to 119 mm in 9 m radius; and greater than 120 cm in 18 m radius.

Sweden National Forest Inventory: The permanent inventory uses a randomly planned regular sampling grid and includes about 4,500 permanent tracts, each surveyed every five years. Plots in the first census were surveyed between 2003 and 2005 and plots in the second census were surveyed between 2008 and 2010. The tracts are rectangular and have different dimensions depending on the location within the country. Each tract has between 4 and 8 circular sample plots. Trees greater than 10 cm d.b.h. are sampled in a 10 m radius.

Finnish National Forest Inventory: We used information from the two consecutives surves of NFI8 sampled in the period 1985-1986 to 1995. The sample plots are in a systematic grid across the country of plot clusters in forested areas (Mäkipää & Heikkinen 2003). In Southern Finland the grid is 16 by 16 square km, with four plots in each cluster at 400 m. intervals, while in Northern Finland the grid is a 24 by 32 km rectangle with three plots per cluster, at 600 m. intervals. These permanent sample plot data were sampled using a variable radius technique with two concentric circular subplots of radius 5.64 m for trees under 10.5 cm of d.b.h. (i.e. 100 m^2) and 9.77 m for trees of d.b.h. 10.5 cm or higher (i.e. 300 m^2).

Table 1. Main characteristics of the plot and sampling design of the National Forest Inventories

	Spain	Germany	Wallonia (Belgium)	Sweden	Finland
Survey dates	1986/96, 1997/2007	1986/90, 2001/02	1994/2003, 2008/11	2005/10, 2008/10	1985/86, 1995
Sample plot design	Single sample plots 1 by 1 km grid	Cluster design 4 by 4 km grid (vary) 4 plots in a cluster	Single sample plots 1 by 0.5 km grid	Cluster design Vary	Cluster design 16 by 16 km grid (vary) 10, 11, 14 plots in a cluster.
Sample tree survey design	Variable radius	Angle-count	Variable radius	Variable radius	Variable radius
Plot size (m^2)	79, 315, 707, 1964	BAF = 4 m^2 ha^{-1}	63, 254, 1017	38, 314	100, 300
Minimum tree d.b.h. (cm)	7.5	10, 7	6.4	4	1

References

Kändler, G. (2009). The design of the second German National Forest Inventory. Proceedings of the eighth annual forest inventory and analysis symposium; 2006 October 16-19; Monterey, CA. Gen. Tech. Report WO-79. Washington, DC: U.S. Department of Agriculture, Forest Service. 19-24

Mäkipää R, Heikkinen J. 2003. Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. *J. Veg. Sci.*, 14, 497-508.

Villaescusa, R. & Díaz, R. (1998). *Segundo Inventario Forestal Nacional (1986-1996).* Ministerio de Medio Ambiente, ICONA, Madrid.

Villanueva, J.A. (2004). *Tercer Inventario Forestal Nacional (1997-2007). Comunidad de Madrid*. Ministerio de Medio Ambiente, Madrid.

Table S1. List of species names, genus and family and forest type.
We followed the nomenclature of *Atlas Florae Europaea*. The forest types are based on the leaf type (i.e. BL: broad-leaved, NL: needle-leaved, DEC: deciduous, EVE: evergreen) and Mediterranean character (i.e. med).

Name	**Genus**	**Family**	**Forest type**
Abies alba Mill.	*Abies*	*Pinaceae*	NL-EVE
Abies grandis (D.Don) Lindl.	*Abies*	*Pinaceae*	NL-EVE
Abies pinsapo Boiss.	*Abies*	*Pinaceae*	NL-EVE
Abies procera Rehder	*Abies*	*Pinaceae*	NL-EVE
Abies spp.	*Abies*	*Pinaceae*	NL-EVE
Acacia dealbata Link	*Acacia*	*Leguminosae*	BL-EVE
Acacia melanoxylon R.Br.	*Acacia*	*Leguminosae*	BL-EVE
Acacia spp.	*Acacia*	*Leguminosae*	BL-EVE
Acer campestre L.	*Acer*	*Aceraceae*	BL-DEC
Acer monspessulanum L.	*Acer*	*Aceraceae*	BL-DEC
Acer negundo L.	*Acer*	*Aceraceae*	BL-DEC
Acer opalus Mill.	*Acer*	*Aceraceae*	BL-DEC
Acer platanoides L.	*Acer*	*Aceraceae*	BL-DEC
Acer pseudoplatanus L.	*Acer*	*Aceraceae*	BL-DEC
Aesculus hippocastanum L.	*Aesculus*	*Hippocastanaceae*	BL-DEC
Alnus glutinosa (L.) Gaertn.	*Alnus*	*Betulaceae*	BL-DEC
Alnus incana (L.) Moench	*Alnus*	*Betulaceae*	BL-DEC
Alnus spp.	*Alnus*	*Betulaceae*	BL-DEC
Alnus viridis (Chaix) DC.	*Alnus*	*Betulaceae*	BL-DEC
Arbutus canariensis Veill.	*Arbutus*	*Ericaceae*	BL-EVE
Arbutus unedo L.	*Arbutus*	*Ericaceae*	BL-EVE
Betula pendula Roth	*Betula*	*Betulaceae*	BL-DEC
Betula pubescens Ehrh.	*Betula*	*Betulaceae*	BL-DEC
Betula spp.	*Betula*	*Betulaceae*	BL-DEC
Carpinus betulus L.	*Carpinus*	*Betulaceae*	BL-DEC
Castanea sativa Mill.	*Castanea*	*Fagaceae*	BL-DEC
Cedrus atlantica (Endl.) Carrière	*Cedrus*	*Pinaceae*	NL-EVE
Cedrus deodara (D.Don) G.Don	*Cedrus*	*Pinaceae*	NL-EVE
Cedrus libani A.Rich.	*Cedrus*	*Pinaceae*	NL-EVE
Celtis australis L.	*Celtis*	*Ulmaceae*	BL-DEC
Ceratonia siliqua L.	*Ceratonia*	*Leguminosae*	BL-EVE
Chamaecyparis lawsoniana (A.Murray bis) Parl.	*Chamaecyparis*	*Cupressaceae*	NL-EVE
Corylus avellana L.	*Corylus*	*Betulaceae*	BL-DEC
Crataegus monogyna Jacq.	*Crataegus*	*Rosaceae*	BL-DEC
Crataegus spp.	*Crataegus*	*Rosaceae*	BL-DEC
Cupressus arizonica Greene	*Cupressus*	*Cupressaceae*	NL-EVE
Cupressus lusitanica Mill.	*Cupressus*	*Cupressaceae*	NL-EVE
Cupressus macrocarpa Hartw.	*Cupressus*	*Cupressaceae*	NL-EVE
Cupressus sempervirens L.	*Cupressus*	*Cupressaceae*	NL-EVE
Erica arborea L.	*Erica*	*Ericaceae*	NL-EVE
Eucalyptus camaldulensis Dehnh.	*Eucalyptus*	*Myrtaceae*	BL-EVE

Name	**Genus**	**Family**	**Forest type**
Eucalyptus globulus Labill.	*Eucalyptus*	*Myrtaceae*	BL-EVE
Eucalyptus gomphocephalus DC.	*Eucalyptus*	*Myrtaceae*	BL-EVE
Eucalyptus nitens (H.Deane & Maiden) Maiden	*Eucalyptus*	*Myrtaceae*	BL-EVE
Eucalyptus viminalis Labill.	*Eucalyptus*	*Myrtaceae*	BL-EVE
Fagus sylvatica L.	*Fagus*	*Fagaceae*	BL-DEC
Ficus carica L.	*Ficus*	*Moraceae*	BL-DEC
Frangula alnus Mill.	*Frangula*	*Rhamnaceae*	BL-DEC
Fraxinus americana L.	*Fraxinus*	*Oleaceae*	BL-DEC
Fraxinus angustifolia Vahl	*Fraxinus*	*Oleaceae*	BL-DEC
Fraxinus excelsior L.	*Fraxinus*	*Oleaceae*	BL-DEC
Fraxinus ornus L.	*Fraxinus*	*Oleaceae*	BL-DEC
Ilex aquifolium L.	*Ilex*	*Aquifoliaceae*	BL-EVE
Ilex canariensis Poir.	*Ilex*	*Aquifoliaceae*	BL-EVE
Juglans regia L.	*Juglans*	*Juglandaceae*	BL-DEC
Juniperus communis L.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus oxycedrus L.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus phoenicea L.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus spp.	*Juniperus*	*Cupressaceae*	NL-EVE
Juniperus thurifera L.	*Juniperus*	*Cupressaceae*	NL-EVE
Larix decidua Mill.	*Larix*	*Pinaceae*	NL-EVE
Larix kaempferi (Lamb.) Carrière sec. Franco	*Larix*	*Pinaceae*	NL-DEC
Larix spp.	*Larix*	*Pinaceae*	NL-EVE
Laurus azorica (Seub.) Franco	*Laurus*	*Lauraceae*	NL-EVE
Laurus nobilis L.	*Laurus*	*Lauraceae*	BL-EVE
Malus sylvestris Mill.	*Malus*	*Rosaceae*	BL-DEC
Morus spp.	*Morus*	*Moraceae*	BL-DEC
Myrica faya Aiton	*Myrica*	*Myricaceae*	BL-EVE
Olea europaea L.	*Olea*	*Oleaceae*	BL-EVE
Persea indica (L.) Spreng.	*Persea*	*Lauraceae*	BL-EVE
Phillyrea latifolia L.	*Phillyrea*	*Oleaceae*	BL-EVE
Phoenix spp.	*Phoenix*	*Arecaceae*	BL-EVE
Picconia excelsa (Aiton) DC.	*Picconia*	*Oleaceae*	BL-EVE
Picea abies (L.) H.Karst.	*Picea*	*Pinaceae*	NL-EVE
Picea omorika (PancKicA) Purk.	*Picea*	*Pinaceae*	NL-EVE
Picea pungens Engelm.	*Picea*	*Pinaceae*	NL-EVE
Picea sitchensis (Bong.) Carrière	*Picea*	*Pinaceae*	NL-EVE
Picea spp.	*Picea*	*Pinaceae*	NL-EVE
Pinus canariensis Sweet ex Spreng.	*Pinus*	*Pinaceae*	NL-EVE
Pinus contorta Douglas ex Loudon	*Pinus*	*Pinaceae*	NL-EVE
Pinus halepensis Mill.	*Pinus*	*Pinaceae*	NL-EVE$_{med}$
Pinus mugo Turra	*Pinus*	*Pinaceae*	NL-EVE
Pinus nigra J.F.Arnold	*Pinus*	*Pinaceae*	NL-EVE
Pinus pinaster Aiton	*Pinus*	*Pinaceae*	NL-EVE$_{med}$
Pinus pinea L.	*Pinus*	*Pinaceae*	NL-EVE$_{med}$

Name	**Genus**	**Family**	**Forest type**
Pinus ponderosa Douglas ex P.Lawson & C.Lawson	*Pinus*	*Pinaceae*	NL-EVE
Pinus radiata D.Don	*Pinus*	*Pinaceae*	NL-EVE
Pinus spp.	*Pinus*	*Pinaceae*	NL-EVE
Pinus strobus L.	*Pinus*	*Pinaceae*	NL-EVE
Pinus sylvestris L.	*Pinus*	*Pinaceae*	NL-EVE
Pinus uncinata Mill. ex Mirb.	*Pinus*	*Pinaceae*	NL-EVE
Pistacia terebinthus L.	*Pistacia*	*Anacardiaceae*	BL-DEC
Platanus hispanica Ten.	*Platanus*	*Platanaceae*	BL-DEC
Populus alba L.	*Populus*	*Salicaceae*	BL-DEC
Populus balsamifera Brayshaw	*Populus*	*Salicaceae*	BL-DEC
Populus nigra L.	*Populus*	*Salicaceae*	BL-DEC
Populus spp.	*Populus*	*Salicaceae*	BL-DEC
Populus tremula L.	*Populus*	*Salicaceae*	BL-DEC
Populus x canadensis Moench	*Populus*	*Salicaceae*	BL-DEC
Prunus avium L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus lusitanica L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus padus L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus serotina Ehrh.	*Prunus*	*Rosaceae*	BL-DEC
Prunus spinosa L.	*Prunus*	*Rosaceae*	BL-DEC
Prunus spp.	*Prunus*	*Rosaceae*	BL-DEC
Pseudotsuga menziesii (Mirb.) Franco	*Pseudotsuga*	*Pinaceae*	NL-EVE
Pyrus spp.	*Pyrus*	*Rosaceae*	BL-DEC
Quercus canariensis Willd.	*Quercus*	*Fagaceae*	BL-DEC
Quercus faginea Lam.	*Quercus*	*Fagaceae*	BL-DEC
Quercus ilex L.	*Quercus*	*Fagaceae*	BL-EVE$_{\text{med}}$
Quercus palustris Münchh.	*Quercus*	*Fagaceae*	BL-DEC
Quercus petraea (Matt.) Liebl.	*Quercus*	*Fagaceae*	BL-DEC
Quercus pubescens Willd. (Q. Humilis)	*Quercus*	*Fagaceae*	BL-DEC
Quercus pyrenaica Willd.	*Quercus*	*Fagaceae*	BL-DEC
Quercus robur L.	*Quercus*	*Fagaceae*	BL-DEC
Quercus rubra L.	*Quercus*	*Fagaceae*	BL-DEC
Quercus spp.	*Quercus*	*Fagaceae*	BL-DEC
Quercus suber L.	*Quercus*	*Fagaceae*	BL-EVE$_{\text{med}}$
Rhamnus alaternus L.	*Rhamnus*	*Rhamnaceae*	BL-EVE
Robinia pseudacacia L.	*Robinia*	*Leguminosae*	BL-DEC
Salix alba L.	*Salix*	*Salicaceae*	BL-DEC
Salix atrocinerea Brot.	*Salix*	*Salicaceae*	BL-DEC
Salix caprea L.	*Salix*	*Salicaceae*	BL-DEC
Salix elaeagnos Scop.	*Salix*	*Salicaceae*	BL-DEC
Salix fragilis L.	*Salix*	*Salicaceae*	BL-DEC
Salix spp.	*Salix*	*Salicaceae*	BL-DEC
Sambucus nigra L.	*Sambucus*	*Caprifoliaceae*	BL-DEC
Sorbus aria (L.) Crantz	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus aucuparia L.	*Sorbus*	*Rosaceae*	BL-DEC

Name	**Genus**	**Family**	**Forest type**
Sorbus domestica L.	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus intermedia (Ehrh.) Pers.	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus spp.	*Sorbus*	*Rosaceae*	BL-DEC
Sorbus torminalis (L.) Crantz	*Sorbus*	*Rosaceae*	BL-DEC
Tamarix spp.	*Tamarix*	*Tamaricaceae*	NL-EVE
Taxus baccata L.	*Taxus*	*Taxaceae*	NL-EVE
Thuja spp.	*Thuja*	*Cupressaceae*	NL-EVE
Tilia cordata Mill.	*Tilia*	*Tiliaceae*	BL-DEC
Tilia platyphyllos Scop.	*Tilia*	*Tiliaceae*	BL-DEC
Tilia spp.	*Tilia*	*Tiliaceae*	BL-DEC
Tsuga spp.	*Tsuga*	*Pinaceae*	NL-EVE
Ulmus glabra Huds.	*Ulmus*	*Ulmaceae*	BL-DEC
Ulmus minor Mill.	*Ulmus*	*Ulmaceae*	BL-DEC
Ulmus spp.	*Ulmus*	*Ulmaceae*	BL-DEC

Table S2. Functional traits used to compute trait-based diversity indices. Trait type, transformation (when applicable), number of missing data for the 143 species initially considered (i.e. data not available, No. NA) and the sources and references used are given.

Trait	Unit	No. NA	Transformation	Sources and references
Leaf mass per area	g m^2	1		(Cornelissen 1996; Cornelissen *et al.* 1996; Cornelissen *et al.* 1997; Atkin *et al.* 1999; McKenna & Shipley 1999; Medlyn *et al.* 1999; Medlyn & Jarvis 1999; Meziane & Shipley 1999; Niinemets 1999; Fonseca *et al.* 2000; Medlyn *et al.* 2001; Niinemets 2001; Shipley 2002; Shipley & Vu 2002; Cornelissen *et al.* 2003; Loveys *et al.* 2003; McDonald *et al.* 2003; Ogaya & Peñuelas 2003; Poschlod *et al.* 2003; Quested *et al.* 2003; Sack *et al.* 2003; Cornelissen *et al.* 2004; Díaz *et al.* 2004; Sack 2004; Wright *et al.* 2004; Cavender-Bares *et al.* 2006; Cornwell *et al.* 2006; Ogaya & Peñuelas 2006; Preston *et al.* 2006; Sack *et al.* 2006; Wright *et al.* 2006; Ackerly & Cornwell 2007; Campbell *et al.* 2007; Garnier *et al.* 2007; Ogaya & Peñuelas 2007; Coomes *et al.* 2008; Cornwell *et al.* 2008; Kleyer *et al.* 2008; Ogaya & Peñuelas 2008; Pakeman *et al.* 2008; Quero *et al.* 2008b; Reich & Oleksyn 2008; Sardans *et al.* 2008a; Sardans *et al.* 2008b; Cornwell & Ackerly 2009; Fortunel *et al.* 2009; Kattge *et al.* 2009; Pakeman *et al.* 2009; Poorter *et al.* 2009; Reich *et al.* 2009; Freschet *et al.* 2010b, a; Laughlin *et al.* 2010; Ordonez *et al.* 2010a; Ordonez *et al.* 2010b; Willis *et al.* 2010; Onoda *et al.* 2011)
Seed mass	mg	4	Natural log	(Cornelissen 1996; Otto 2002; Díaz *et al.* 2004; Kühn *et al.* 2004; Moles *et al.* 2004; Sack 2004; Moles *et al.* 2005a; Moles *et al.* 2005b; Cornwell *et al.* 2006; Preston *et al.* 2006; Ackerly & Cornwell 2007; Garnier *et al.* 2007; Kew 2008; Kleyer *et al.* 2008; Pakeman *et al.* 2008; Paula & Pausas 2008; Quero *et al.* 2008a; Cornwell & Ackerly 2009; Fortunel *et al.* 2009; Green 2009; Pakeman *et al.* 2009; Paula *et al.* 2009; Laughlin *et al.* 2010)
Wood density	g cm-3	2		(Castro-Díez et al. 1998; Cornelissen *et al.* 2003; Ogaya & Peñuelas 2003; Cornwell *et al.* 2006; Ogaya & Peñuelas 2006; Preston *et al.* 2006; Ackerly & Cornwell 2007; Ogaya & Peñuelas 2007; Kleyer *et al.* 2008; Ogaya & Peñuelas 2008; Sardans *et al.* 2008a; Sardans *et al.* 2008b; Chave *et al.* 2009; Cornwell & Ackerly 2009; Reich *et al.* 2009; Zanne *et al.* 2009; Ordonez *et al.* 2010a; Ordonez *et al.* 2010b)
Maximum tree height	m	0		Tree height was calculated as the 99.99 % percentile of the distribution of tree heights measured for each species from the first census of each National Forest Inventory (see Appendix S1).
Water potential causing 50% of hydraulic loss	Mpa	8		(Choat *et al.* 2012)

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Table S3. Estimated parameters and standard errors for the best models predicting changes in multidimensional functional space ((A) first axis of PCA, and (B) second axis of PCA)) for forest type, including: broad-leaved-deciduous (BLDEC), needle-leaved evergreen (NLEVE), broad-leaved evergreen (BLEVEm), and Mediterranean needle-leaved evergreen (NLEVEm).

		(A) PC1 (Eq. (1))*			
Variables	**Par. Eq. 1**	**BLDEC**	**NLEVE**	**BLEVEm**	**NLEVEm**
WAI	β_1	-0.1975 (0.0202)	-0.0661 (0.0117)	0.3254 (0.0558)	0.3482 (0.0375)
TA	β_2	0.2241 (0.0185)	-0.1195 (0.0119)	0.0924 (0.1079)	0.1218 (0.0547)
ID	β_3	0.0331 (0.0182)	0.0164 (0.0131)	0.0755 (0.0394)	0.0306 (0.0369)
TD	β_4	0.0811 (0.0195)	-0.0724 (0.0134)	0.1705 (0.0544)	-0.1354 (0.0421)
DBH	β_5	0.0582 (0.0175)	0.085 (0.0135)	0.3095 (0.0509)	0.1349 (0.0544)
FD	β_6	0.0796 (0.0124)	0.1197 (0.0104)	0.121 (0.0235)	0.1328 (0.0237)
WAI × TD	β_7	0.0905 (0.0245)	-0.0275 (0.0139)	0.1061 (0.0522)	-0.0252 (0.0332)
TA × TD	β_8	0.0911 (0.02)	0.0094 (0.012)	-0.0536 (0.0702)	0.0644 (0.0411)
WAI × DBH	β_9	0.0958 (0.0231)	-0.0115 (0.0137)	0.0834 (0.0559)	0.1964 (0.0416)
TA × DBH	β_{10}	0.0847 (0.0181)	-0.0753 (0.0118)	-0.0622 (0.0703)	0.0884 (0.0492)
ID × DBH	β_{11}	0.0483 (0.0141)	-0.0215 (0.0117)	0.1155 (0.0235)	-0.0655 (0.0338)
WAI × FD	β_{12}	-0.0523 (0.0157)	-0.0745 (0.0121)	0.0766 (0.0271)	0.19 (0.0188)
TA × FD	β_{13}	-0.1902 (0.0134)	-0.1277 (0.0095)	-0.0539 (0.0388)	0.0951 (0.0337)
ID × FD	β_{14}	-0.0442 (0.0118)	-0.0774 (0.0103)	-0.0178 (0.0184)	-0.0851 (0.0216)
WAI × ID	β_{15}	-0.0788 (0.0241)	0.0019 (0.0136)	0.181 (0.0503)	0.1059 (0.0412)
WAI × TA	β_{16}	0.1761 (0.0241)	0.0372 (0.0135)	-0.0031 (0.0883)	-0.0584 (0.0495)
TA × ID	β_{17}	0.1519 (0.0192)	0.0227 (0.011)	0.1619 (0.0543)	-0.0152 (0.043)

$$PC1 = \underline{\beta_1}(\mathrm{WAI}) + \underline{\beta_2}(\mathrm{TA}) + \underline{\beta_3}(\mathrm{ID}) + \underline{\beta_4}(TD) + (\underline{\beta_5}(\mathrm{DBH}) + \underline{\beta_6}(\mathrm{FD}) + \underline{\beta_7}(\mathrm{WAI})(\mathrm{TD}) + \underline{\beta_8}(\mathrm{TA})(\mathrm{TD}) + \underline{\beta_9}(\mathrm{WAI})(\mathrm{DBH}) + \underline{\beta_{10}}(\mathrm{TA})(\mathrm{DBH}) + \underline{\beta_{11}}(\mathrm{ID})(\mathrm{DBH}) + \underline{\beta_{12}}(\mathrm{WAI})(\mathrm{FD}) + \underline{\beta_{13}}(\mathrm{TA})(\mathrm{FD}) + \underline{\beta_{14}}(\mathrm{ID})(\mathrm{FD}) + \underline{\beta_{15}}(\mathrm{WAI})(\mathrm{TA}) + \underline{\beta_{16}}(\mathrm{TA})(\mathrm{ID}) + \underline{\beta_{17}}(\mathrm{WAI})(\mathrm{ID}) \qquad \textbf{Eq. (1)*}$$

		(B) PC2 (Eq (2))*			
Variables	**Par. Eq. 2**	**BLDEC**	**NLEVE**	**BLEVE**	**NLEVEm**
WAI	β_1	-0.0525 (0.0128)	-0.0026 (0.0075)	-0.0618 (0.0356)	-0.4988 (0.0239)
TA	β_2	-0.0069 (0.0117)	0.017 (0.0075)	-0.0368 (0.0686)	-0.3408 (0.0347)
ID	β_3	-0.0298 (0.0116)	0.0141 (0.0084)	-0.0003 (0.0256)	0.1145 (0.0238)
TD	β_4	0.0021 (0.0124)	0.0107 (0.0086)	-0.0517 (0.0346)	0.2035 (0.0272)
DBH	β_5	0.127 (0.0111)	-0.0301 (0.0086)	-0.0211 (0.0325)	0.1518 (0.0346)
FD	β_6	-0.1511 (0.0079)	-0.0965 (0.0066)	-0.0817 (0.015)	-0.1399 (0.015)
WAI × TD	β_7	0.045 (0.0158)	0.0326 (0.0093)	-0.0131 (0.0339)	0.0115 (0.0214)
TA × TD	β_8	-0.0146 (0.0132)	-0.0259 (0.0077)	0.0326 (0.0463)	-0.1003 (0.0276)
ID × TD	β_9	0.0508 (0.0131)	-0.0287 (0.0093)	0.0017 (0.0224)	0.0309 (0.0228)
WAI × DBH	β_{10}	0.088 (0.0147)	0.0432 (0.0088)	-0.0309 (0.0361)	-0.1657 (0.0265)
TA × DBH	β_{11}	-0.0029 (0.0117)	0.0029 (0.0075)	0.0079 (0.0459)	-0.1556 (0.032)
ID × DBH	β_{12}	0.074 (0.0118)	-0.0122 (0.0086)	0.0189 (0.0222)	0.154 (0.0263)
WAI × FD	β_{13}	-0.0538 (0.01)	-0.0419 (0.0077)	-0.1569 (0.0172)	-0.2327 (0.012)
TA × FD	β_{14}	0.0439 (0.0085)	-0.0138 (0.006)	-0.059 (0.0247)	-0.0929 (0.0214)
ID × FD	β_{15}	0.0081 (0.0075)	-0.0332 (0.0065)	0.0389 (0.0117)	0.0222 (0.0138)
WAI × ID	β_{16}	-0.0025 (0.0154)	0.0083 (0.0087)	-0.0066 (0.033)	-0.1075 (0.0269)
WAI × TA	β_{17}	-0.0415 (0.0153)	-0.0188 (0.0086)	-0.0426 (0.0572)	0.0332 (0.0315)
TA × ID	β_{18}	0.0008 (0.0123)	-0.0035 (0.0072)	0.0067 (0.0347)	-0.1552 (0.0274)

$$PC2 = \underline{\beta_1}(\mathrm{WAI}) + \underline{\beta_2}(\mathrm{TA}) + \underline{\beta_3}(\mathrm{ID}) + \underline{\beta_4}(\mathrm{TD}) + \underline{\beta_5}(\mathrm{DBH}) + \underline{\beta_6}(\mathrm{FD}) + \underline{\beta_7}(\mathrm{WAI})(\mathrm{TD}) + \underline{\beta_8}(\mathrm{TA})(\mathrm{TD}) + \underline{\beta_9}(\mathrm{ID})(\mathrm{TD}) + \underline{\beta_{10}}(\mathrm{WAI})(\mathrm{DBH}) + \underline{\beta_{11}}(\mathrm{TA})(\mathrm{DBH}) + \underline{\beta_{12}}(\mathrm{ID})(\mathrm{DBH}) + \underline{\beta_{13}}(\mathrm{WAI})(\mathrm{FD}) + \underline{\beta_{14}}(\mathrm{TA})(\mathrm{FD}) + \underline{\beta_{15}}(\mathrm{ID})(\mathrm{FD}) + \underline{\beta_{16}}(\mathrm{WAI})(\mathrm{TA}) + \underline{\beta_{17}}(\mathrm{WAI})(\mathrm{ID}) + \underline{\beta_{18}}(\mathrm{TA})(\mathrm{ID}) \qquad \textbf{Eq. (2)*}$$

Table S4. Conditional independence test applied via d-sep method, for all forest types together and each forest type separately. {Var1, Var2}|{Var$_k$} means that variables 1 and 2 are and independent conditional claim (i.e. Var$_1$ does not imply a variation in Var$_2$ if Var$_k$ is held constant). The p-value is obtained by comparing the value of the C statistic for each hypothesis to a chi-square distribution with the same degrees of freedom (a hypothesis is rejected if the C statistic is statistically different from the χ^2 value).

Claim No.	**d-sep claim of independence**	**Model**	**H0**	**P value**				
				All forests	**BLDEC**	**NLEVE**	**NLEVEm**	**BLEVEm**
C1	{STD,DBH}|{WAI, TA, ID}	DBH ~ TD + WAI + TA + ID	TD = 0	0.0000	0.0000	0.0000	0.0000	0.0000
C2	{STD,FD}|{WAI, TA, ID}	TD ~ FD + WAI + TA + ID	FD = 0	0.0000	0.0000	0.0145	0.0842	0.0000
C3	{FD,DBH}|{WAI, TA, ID}	DBH ~ FD + WAI + TA + ID	FD = 0	0.0003	0.0720	0.0000	0.0000	0.0000
C4	{M,G}|{WAI, TA, ID, TD, DBH, FD}	G ~ M + WAI + TA + ID + TD + DBH + FD	M = 0	0.0000	0.0000	0.0000	0.0000	0.0006
C5	{PCA1,PCA2}|{M,G}	PCA1 ~ PCA2 + M + G	PCA = 0	0.0039	0.0061	0.0000	0.0000	0.0000
C6	{PCA1,WAI}| {G, M}	PCA1 ~ WAI + M + G	WAI = 0	0.6911	0.0000	0.0000	0.0000	0.0000
C7	{PCA1,TA}| {G, M}	PCA1 ~ TA + M + G	TA = 0	0.6763	0.2403	0.5161	0.0000	0.6136
C8	{PCA1,ID}| {G, M}	PCA1 ~ ID + M + G	ID = 0	0.3560	0.0463	0.2902	0.0000	0.1526
C9	{PCA1,TD}|{WAI, TA, ID, G, M}	PCA1 ~ TD + WAI + TA + ID + M + G	TD = 0	0.0000	0.0000	0.0000	0.0000	0.2866
C10	{PCA1,DBH}|{WAI, TA, ID, G, M}	PCA1 ~ DBH + WAI + TA + ID + M + G	DBH = 0	0.0006	0.0000	0.0000	0.8889	0.1551
C11	{PCA1,FD}|{WAI, TA, ID, G, M}	PCA1 ~ FD + WAI + TA + ID + M + G	FD = 0	0.0000	0.0000	0.0000	0.0000	0.0000
C12	{PCA2,WAI}| {G, M}	PCA2 ~ WAI + M + G	WAI = 0	0.0000	0.0997	0.0060	0.0000	0.0000
C13	{PCA2,TA}| {G, M}	PCA2 ~ TA + M + G	TA = 0	0.0006	0.9234	0.1303	0.0000	0.7192
C14	{PCA2,ID}| {G, M}	PCA2 ~ ID + M + G	ID = 0	0.7975	0.5052	0.1215	0.0000	0.3568
C15	{PCA2,TD}|{WAI, TA, ID, G, M}	PCA2 ~ TD + WAI + TA + ID + M + G	TD = 0	0.0000	0.0000	0.0000	0.0000	0.6716
C16	{PCA2,DBH}|{WAI, TA, ID, G, M}	PCA2 ~ DBH + WAI + TA + ID + M + G	DBH = 0	0.3820	0.2785	0.0001	0.0009	0.1924
C17	{PCA2,FD}|{WAI, TA, ID, G, M}	PCA2 ~ FD + WAI + TA + ID + M + G	FD = 0	0.0000	0.0000	0.0000	0.0000	0.0000
			C- statistic	2373.43	1392.19	1869.87	2726.21	1428.22
			P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
			AIC	2479.43	1498.19	1975.87	2804.21	1506.22

The model was fitted for all forest types together and each forest type separately (i.e. BLDEC: broadleaved-deciduous; NLEVE: Needle-leaved evergreen; BLEVEm: Broadleaved evergreen Mediterranean; and NLEVEm: Needle-leaved evergreen Mediterranean) including the random effect of cluster identity nested in plot when applicable. C is the Fisher C statistics, the p-value and the AIC of the model.

Table S5. Standardised regression coefficients of piecewise structural equation models fitted (see Fig S6). The parameter estimate (Est.), standard errors (SE) and p-values (P) are also shown.

		All forests		BLDEC		NELEVE		NLEVEm		BLEVE	
Response	**Predictor**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**
DBH	WAI	0.031 (0.005)	< **0.0001**	0.081 (0.013)	< **0.0001**	0.084 (0.007)	< **0.0001**	0.176 (0.011)	< **0.0001**	-0.558 (0.024)	< **0.0001**
DBH	TA	0.031 (0.006)	< **0.0001**	-0.011 (0.015)	0.4518	0.083 (0.007)	< **0.0001**	0.243 (0.014)	< **0.0001**	-0.487 (0.028)	< **0.0001**
DBH	ID	-0.148 (0.005)	< **0.0001**	-0.141 (0.011)	< **0.0001**	-0.018 (0.006)	**0.0052**	-0.132 (0.011)	< **0.0001**	-0.433 (0.014)	< **0.0001**
TD	WAI	0.168 (0.005)	< **0.0001**	0.067 (0.012)	< **0.0001**	-0.055 (0.007)	< **0.0001**	0.146 (0.012)	< **0.0001**	0.859 (0.023)	< **0.0001**
TD	TA	0.031 (0.006)	< **0.0001**	0.016 (0.014)	0.2497	0.02 (0.006)	**0.0011**	0.032 (0.016)	**0.0409**	0.379 (0.028)	< **0.0001**
TD	ID	0.117 (0.005)	< **0.0001**	0.072 (0.01)	< **0.0001**	0.001 (0.006)	0.8616	0.097 (0.012)	< **0.0001**	0.384 (0.014)	< **0.0001**
FD	WAI	0.081 (0.005)	< **0.0001**	0.113 (0.014)	< **0.0001**	-0.038 (0.007)	< **0.0001**	0.311 (0.013)	< **0.0001**	0.5 (0.026)	< **0.0001**
FD	TA	-0.06 (0.006)	< **0.0001**	-0.092 (0.016)	< **0.0001**	-0.023 (0.007)	**0.0015**	0.033 (0.016)	**0.048**	0.173 (0.031)	< **0.0001**
FD	ID	0.044 (0.005)	< **0.0001**	0.07 (0.011)	< **0.0001**	0.009 (0.007)	0.1649	0.03 (0.013)	**0.019**	0.139 (0.015)	< **0.0001**
G	TD	0.451 (0.004)	< **0.0001**	0.316 (0.008)	< **0.0001**	0.362 (0.006)	< **0.0001**	0.493 (0.01)	< **0.0001**	0.58 (0.018)	< **0.0001**
G	DBH	-0.07 (0.004)	< **0.0001**	-0.046 (0.008)	< **0.0001**	0.129 (0.005)	< **0.0001**	-0.005 (0.012)	0.6601	0.057 (0.018)	**0.0012**
G	FD	0.014 (0.003)	< **0.0001**	0.048 (0.005)	< **0.0001**	-0.13 (0.006)	< **0.0001**	0.018 (0.007)	**0.0149**	0.076 (0.009)	< **0.0001**
G	WAI	0.17 (0.004)	< **0.0001**	0.086 (0.008)	< **0.0001**	-0.016 (0.004)	**0.0004**	0.288 (0.01)	< **0.0001**	0.395 (0.02)	< **0.0001**
G	TA	0.035 (0.005)	< **0.0001**	0.021 (0.01)	**0.0282**	-0.02 (0.006)	**0.0007**	0.226 (0.012)	< **0.0001**	-0.048 (0.022)	**0.0301**
G	ID	0.006 (0.004)	0.1286	-0.004 (0.007)	0.5091	-0.014 (0.005)	**0.0056**	0.045 (0.009)	< **0.0001**	-0.012 (0.011)	0.2732
M	TD	0.54 (0.005)	< **0.0001**	0.439 (0.01)	< **0.0001**	0.594 (0.007)	< **0.0001**	0.547 (0.012)	< **0.0001**	0.353 (0.015)	< **0.0001**
M	DBH	0.414 (0.005)	< **0.0001**	0.355 (0.01)	< **0.0001**	0.435 (0.007)	< **0.0001**	0.509 (0.014)	< **0.0001**	0.337 (0.015)	< **0.0001**
M	FD	0.006 (0.003)	0.0753	0.041 (0.007)	< **0.0001**	0.042 (0.006)	< **0.0001**	0.02 (0.009)	**0.0226**	0.049 (0.008)	< **0.0001**
M	WAI	0.033 (0.004)	< **0.0001**	0.002 (0.011)	0.8291	-0.017 (0.005)	**0.0010**	0.24 (0.012)	< **0.0001**	0.141 (0.017)	< **0.0001**
M	TA	-0.011 (0.005)	**0.0368**	-0.011 (0.012)	0.3744	-0.018 (0.006)	**0.0025**	0.038 (0.015)	**0.0102**	0.026 (0.019)	0.1581
M	ID	-0.026 (0.004)	< **0.0001**	0.007 (0.009)	0.4578	-0.014 (0.007)	**0.0289**	-0.085 (0.011)	< **0.0001**	0.004 (0.01)	0.6547
PCA1	G	-0.088 (0.004)	< **0.0001**	-0.158 (0.014)	< **0.0001**	-0.299 (0.012)	< **0.0001**	-0.035 (0.015)	**0.0186**	-0.088 (0.014)	< **0.0001**
PCA1	M	0.184 (0.004)	< **0.0001**	0.208 (0.012)	< **0.0001**	0.261 (0.011)	< **0.0001**	0.336 (0.013)	< **0.0001**	0.208 (0.023)	< **0.0001**

		All forests		**BLDEC**		**NELEVE**		**NLEVEm**		**BLEVE**	
Response	**Predictor**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**
PCA2	G	-0.043 (0.004)	**< 0.0001**	-0.085 (0.014)	**< 0.0001**	-0.026 (0.006)	**< 0.0001**	-0.076 (0.012)	**< 0.0001**	-0.046 (0.006)	**< 0.0001**
PCA2	M	-0.062 (0.004)	**< 0.0001**	-0.07 (0.011)	**< 0.0001**	-0.026 (0.006)	**< 0.0001**	-0.186 (0.011)	**< 0.0001**	-0.044 (0.01)	**< 0.0001**

The models were fitted for all forest types together and each forest type separately (i.e. BLDEC: broadleaved-deciduous; NLEVE: Needle-leaved evergreen; NLEVEm: Needle-leaved evergreen Mediterranean; and BLEVEm: Broadleaved evergreen Mediterranean) including the random effect of cluster identity nested in plot when applicable. C is the Fisher C statistics, the p-value and the AIC of the model. If the p-value is lower than 0.05 it is marked in bold.

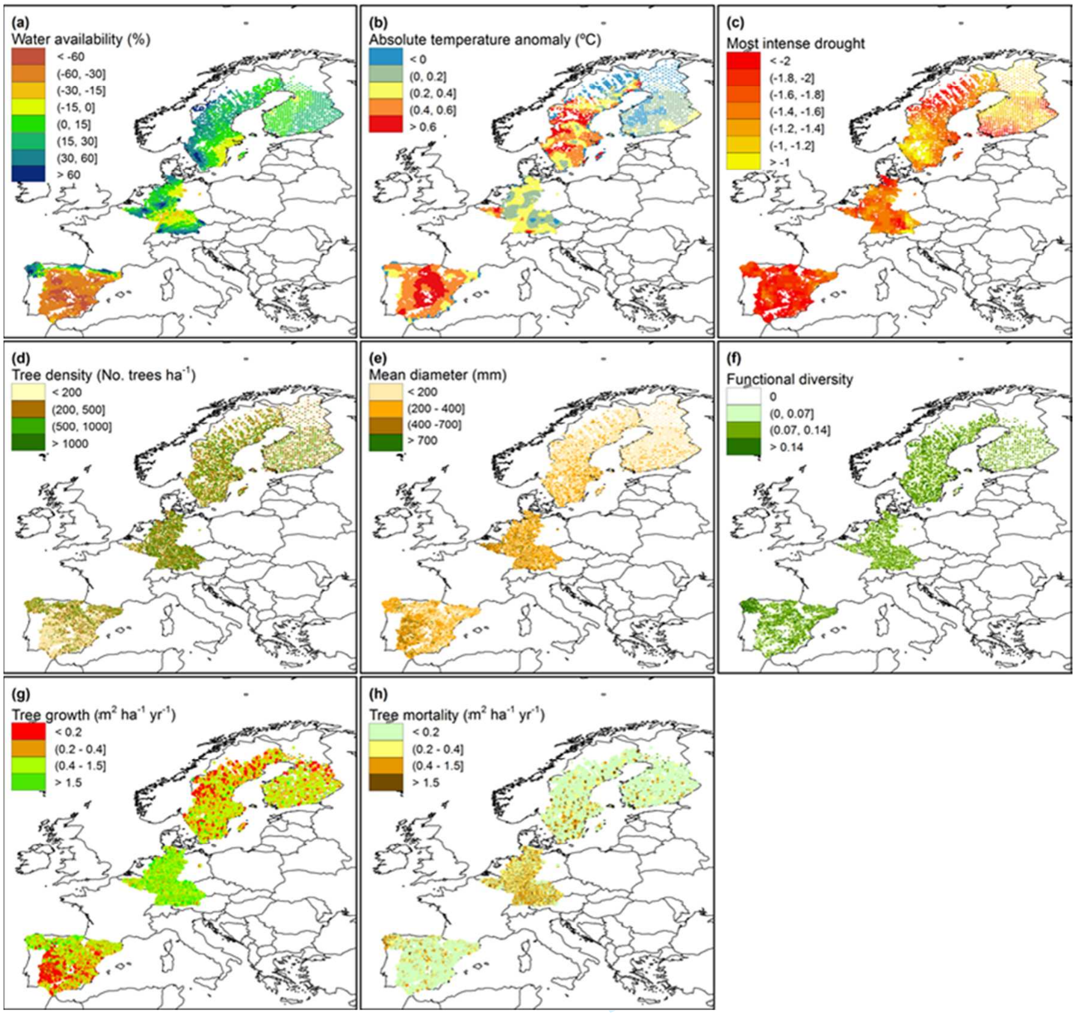

Fig. S1 Spatial distribution of the explanatory variables in the National Forest Inventories related to climate, stand development and tree demography: (a) water availability (%), (b) absolute temperature anomaly (ºC), (c) most intense drought (adimensional), (d) tree density (No. trees ha^{-1}), (e) mean diameter (mm), (f) functional diversity (adimensional), (g) tree growth, and (h) tree mortality.

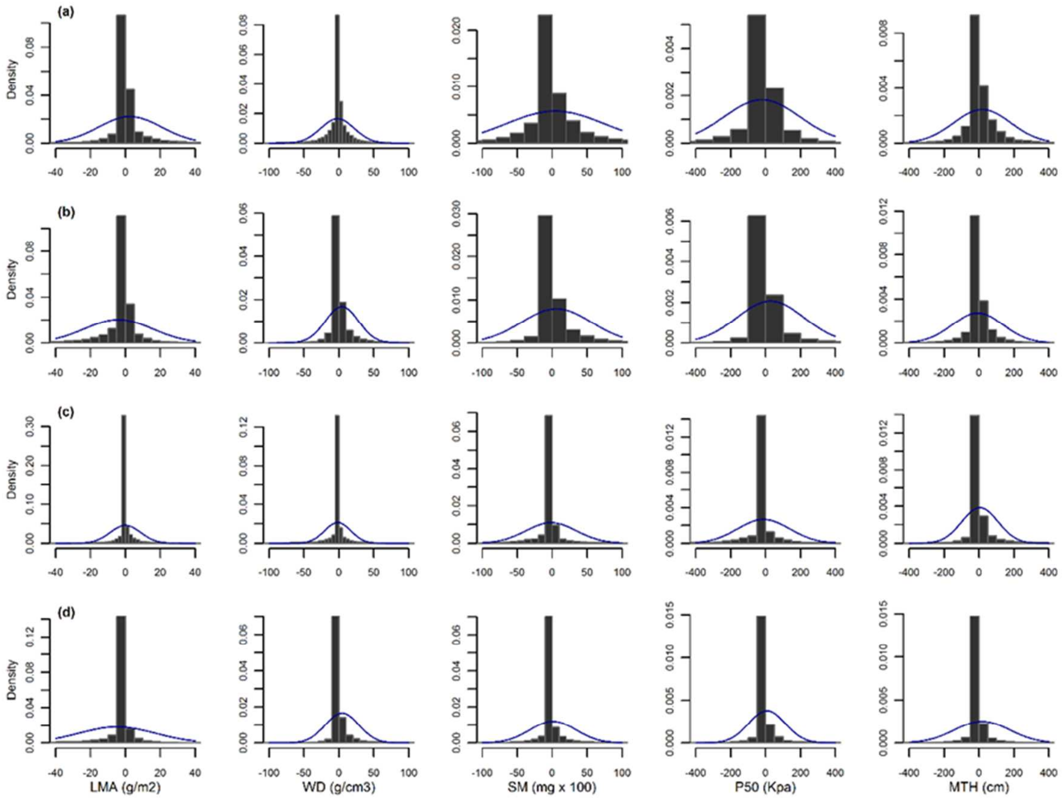

Fig. S2. Histograms and density curves of the changes in functional composition for each functional trait (LMA: leaf mass per area, WD: wood density, SM: seed mass, P50: water potential loss, and MTH: Maximum tree height) and each forest type (a) broad-leaved deciduous, (b) broad-leaved evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen Mediterranean forests.

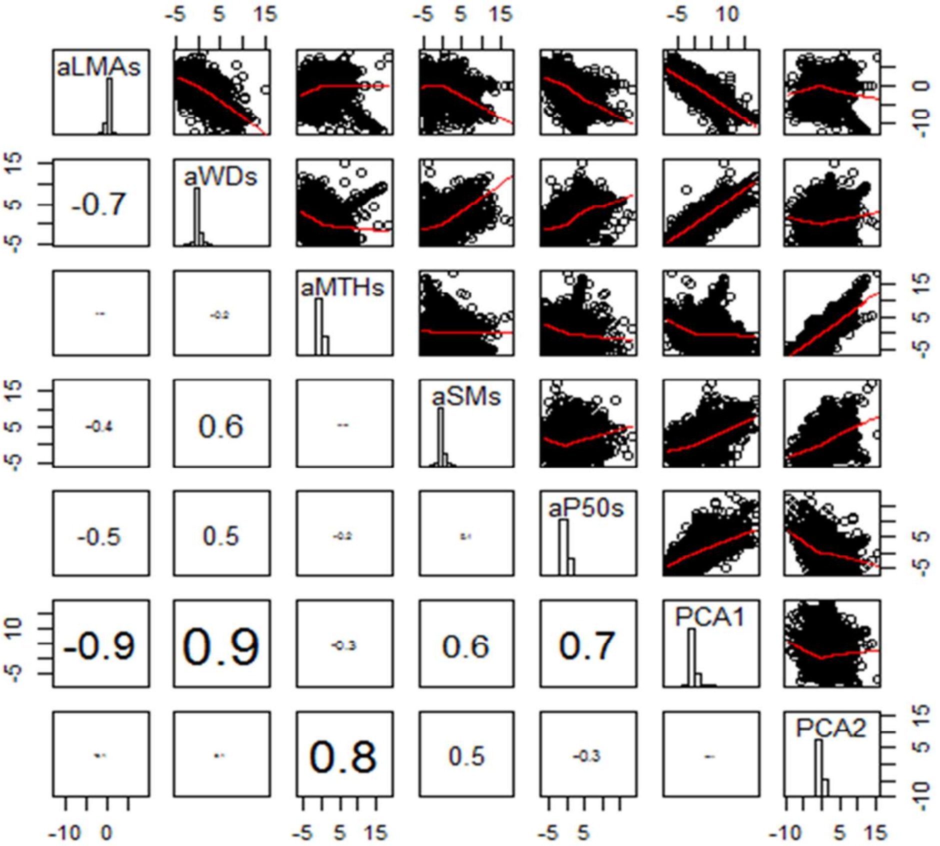

Fig. S3 Results of the Principal Component Analysis of the standardised changes in functional community weighted means, including scatterplots, histograms and correlations between the first two axis of the PCA and the standardised changes in functional identity for each functional trait.

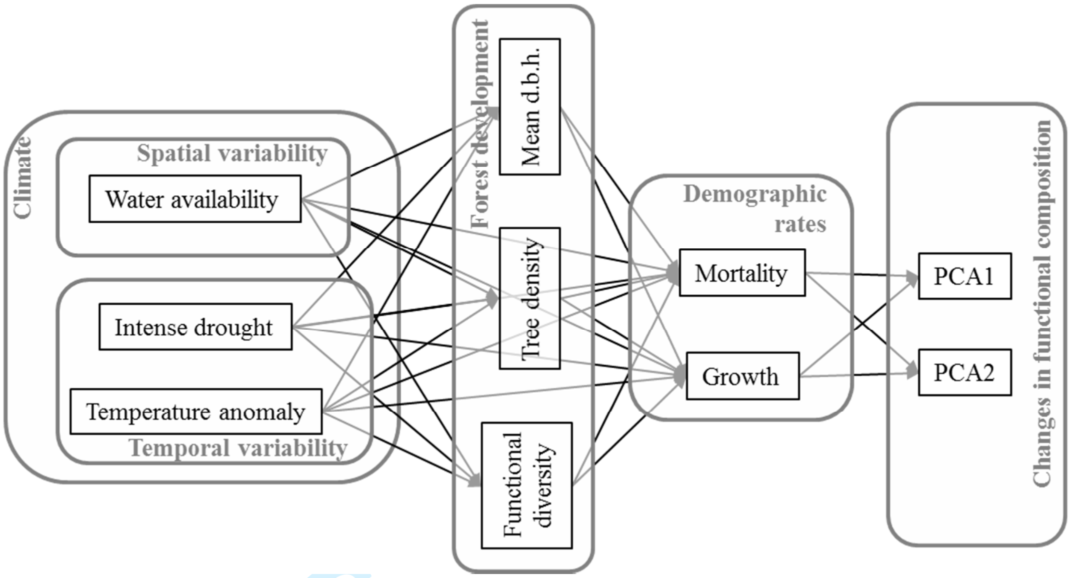

Fig. S4 Acyclic graph showing a schematic representation of variables included in the models testing the effects of climate and stand development through demographic rates on changes in functional composition. Variables in black rectangles represent latent variables while grey rectangles represent categories and subcategories. Lines indicate tested hypotheses and arrows hypothesised direction of causality. Note that if no line is shown the relationship was not tested. The same models were performed for all forest types together and each forest type separately.

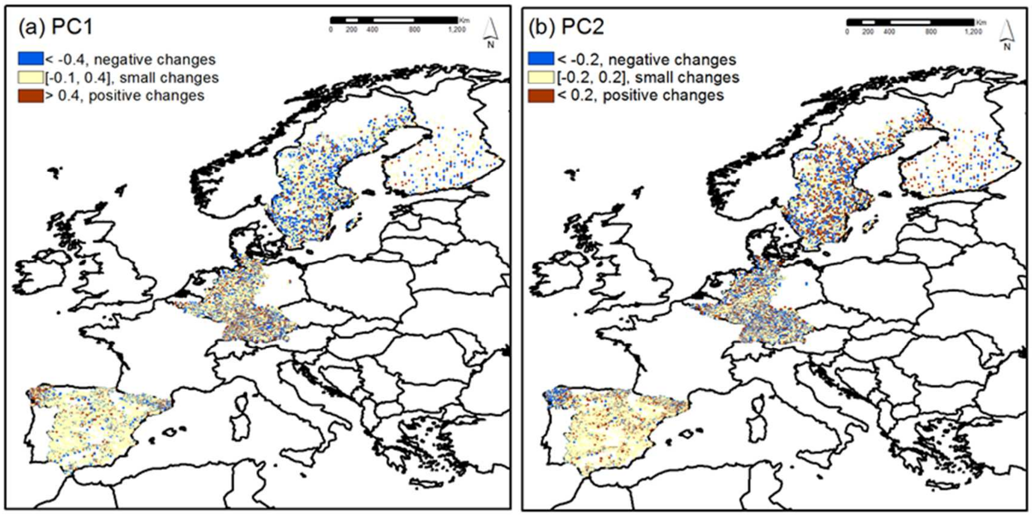

Fig S5. Map of the (a) first and (b) second axis of the Principal Component Analyses performed with the functional traits.

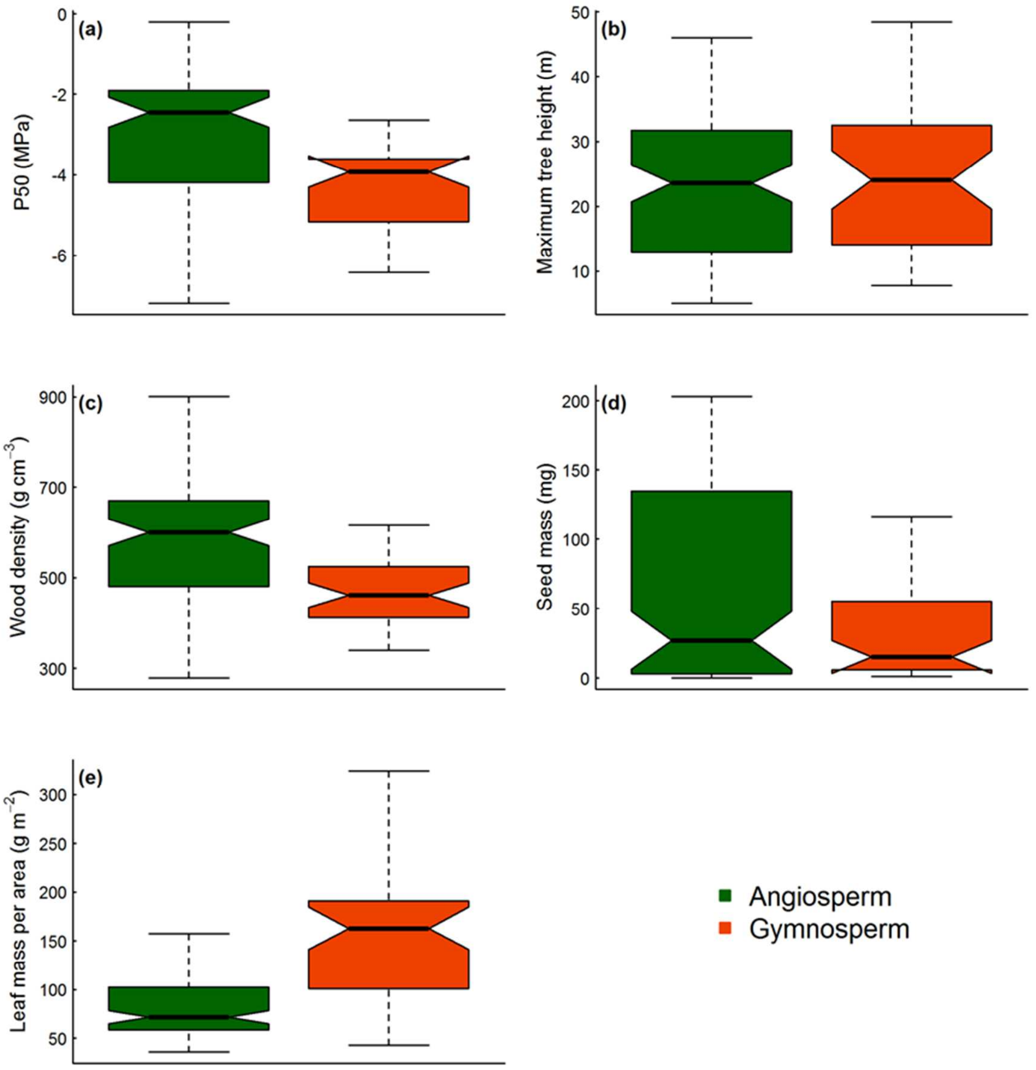

Fig. S6 Box-whisker plots of each of the functional traits for the species present in the European National Forest Inventories used for angiosperms and gymnosperms: (a) water potential causing 50% loss of hydraulic conductivity (P50, MPa), maximum tree height (MTH, m), wood density (WD, g cm^{-3}), seed mass (SM, mg) and leaf mass per area (LMA, g m^{-2}).

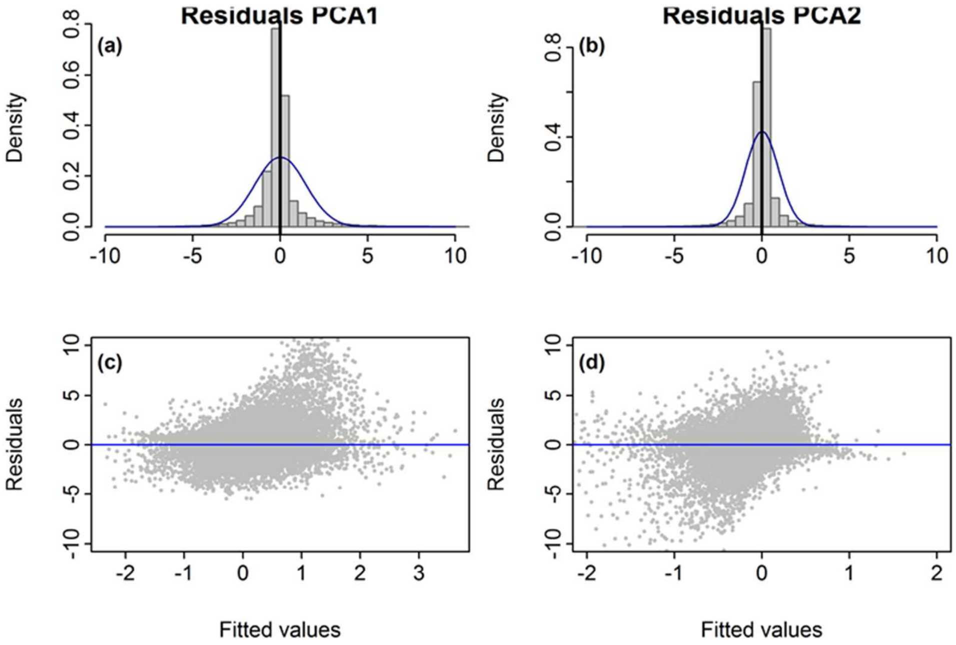

Fig. S7 Histogram of the residuals (a, b) and scatterplot of residuals versus predicted values (c,d) for the best models selected to predict the first and second PCA axis of the multidimensional change in trait space.

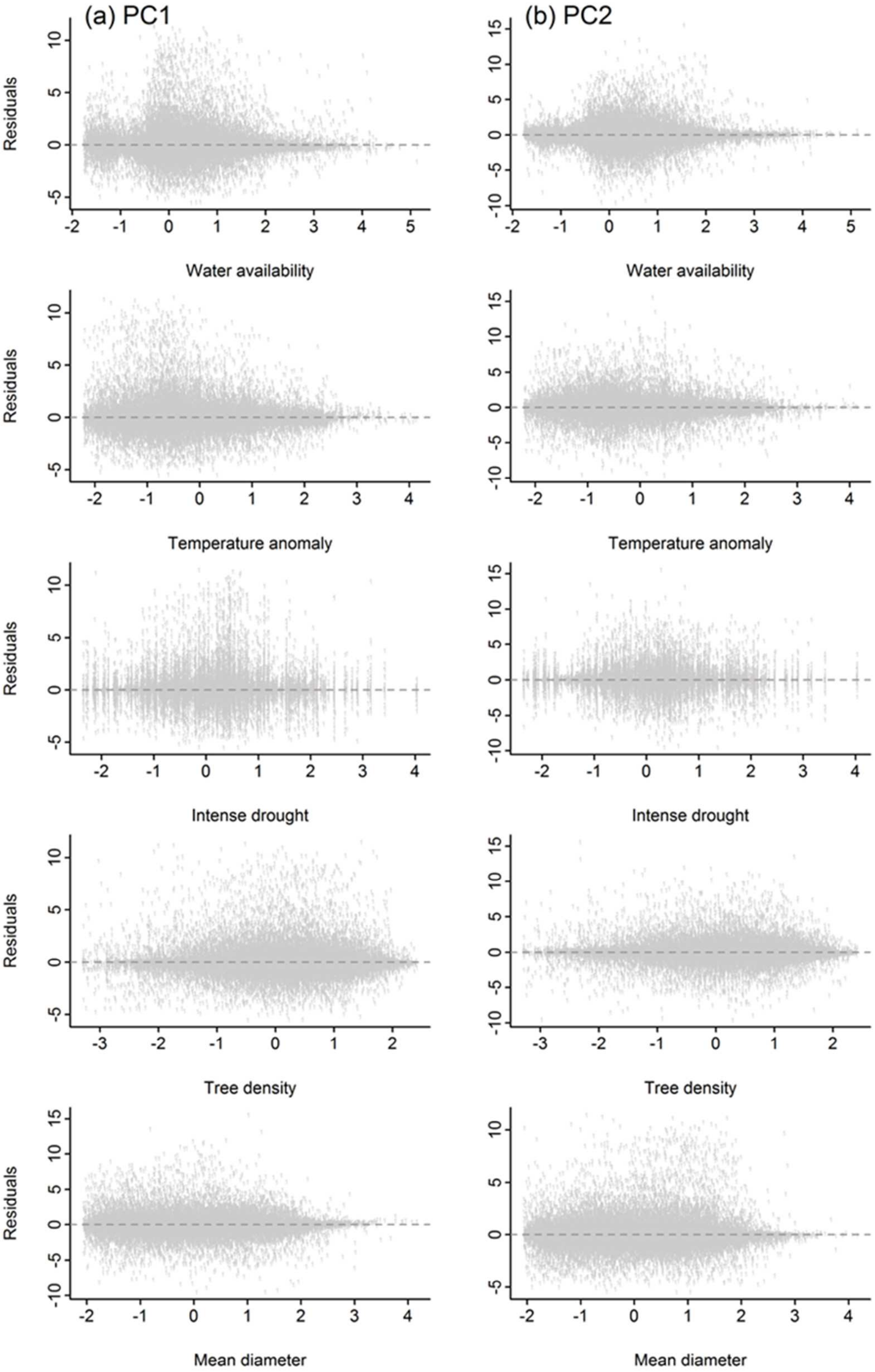

Fig. S8 Partial residual plots for models using as response variable (a) PC1 and (b) PC2.

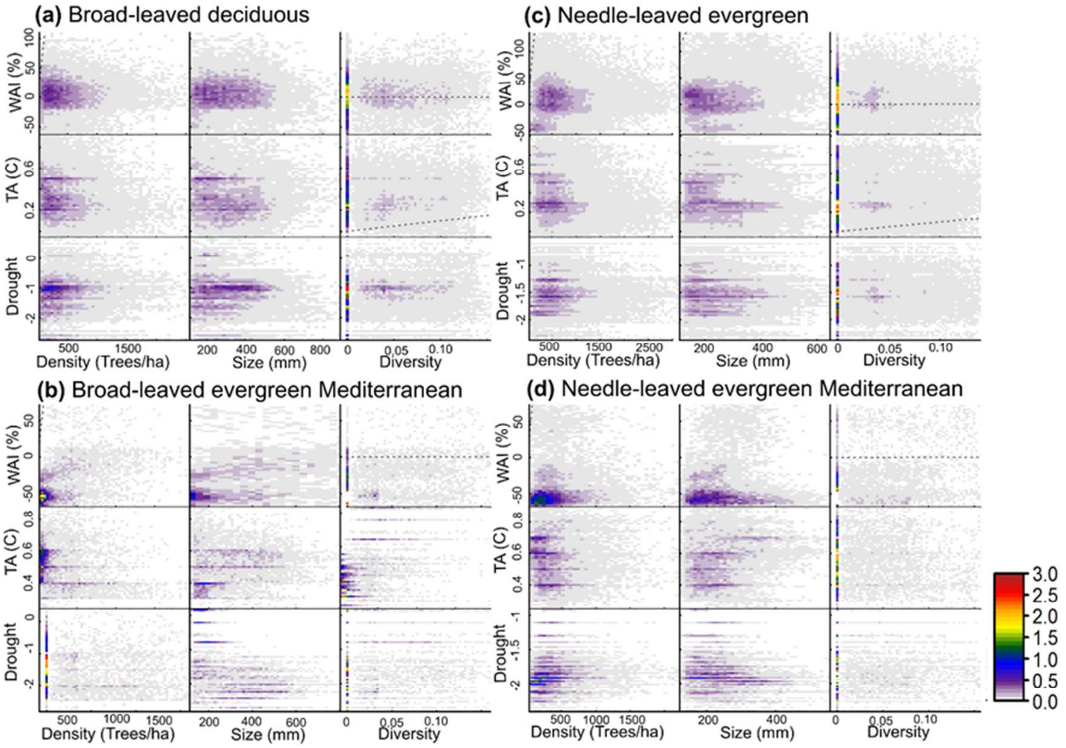

Fig. S9 Density plots of the NFI data along climatic and stand development variables in each forest type studied: (a) broad-leaved deciduous, (b) broad-leaved evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen Mediterranean forests.

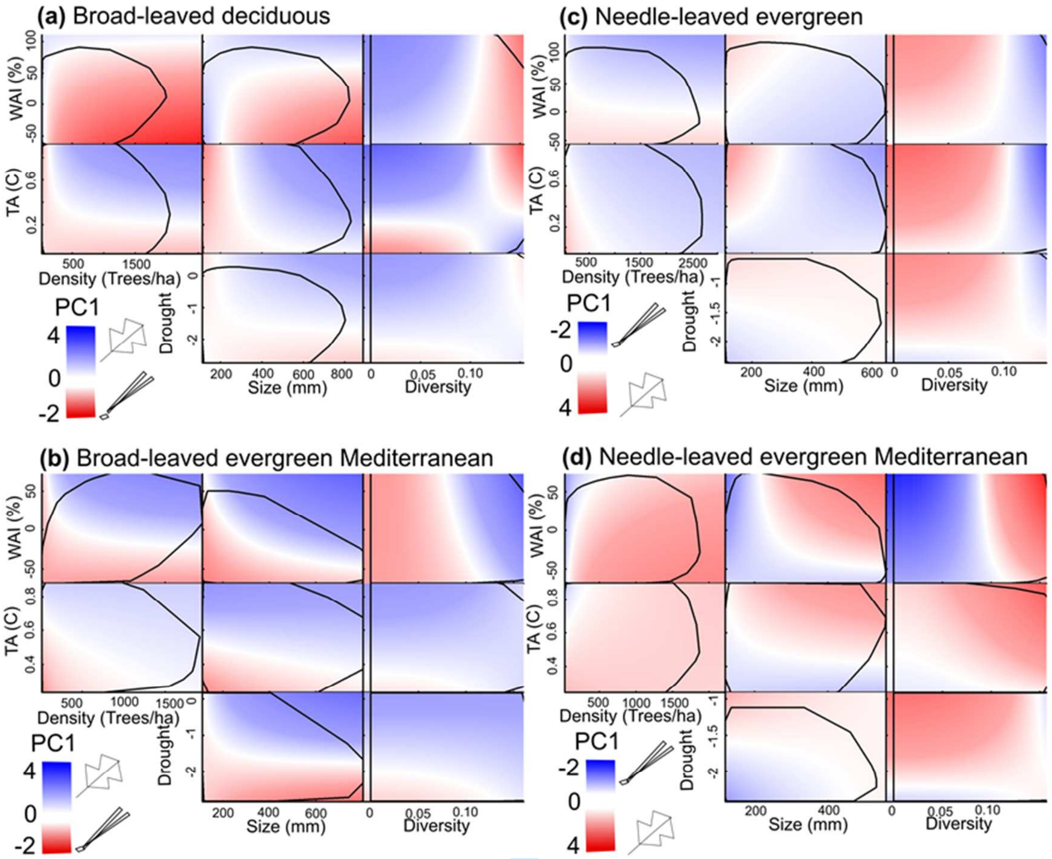

Fig S10 Interactive effects of climatic and structural variables on the first axis of the PCA (PC1) in each forest type studied: (a) broad-leaved deciduous, (b) broad-leaved evergreen, (c) needle-leaved evergreen, and (d) needle-leaved evergreen Mediterranean forests. Blue colour represents changes towards functional strategies similar to the dominant and red colour different than the dominant. Convex hull lines covering the presence of data points in each panel are represented using black lines and density plots are shown in Fig. S9.

Fig. S11 Maximum tree height (maximum and mean value) for main species in the functional groups of each forest type including Mediterranean needle-leaved species (i.e. *Pinus halepensis*, *P. pinea* and *P. pinaster*), Mediterranean broad-leaved evergreen species (i.e. *Quercus ilex* and *Q. suber*), Sub-Mediterranean broad-leaved deciduous species (i.e. *Quercus pyrenaica* and *Q. faginea*), temperate broad-leaved species (i.e. *Fagus sylvatica*, *Quercus robur*, *Q. petraea* and *Castanea sativa*) and other conifers (i.e. *Abies* sp., *Picea* sp. and *Pinus sylvestris*).