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

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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 recent 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 (partially related to the trait differences between angiosperms and gymnosperms), 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. towards late-successional short-statured hardwoods in Mediterranean forests and taller gymnosperms in boreal forests) and latitudinal gradients (e.g. larger proportion of gymnosperm-like strategies at low water availability in forests formerly dominated by broad-leaved deciduous species). Recent climate change generally favoured the dominance of angiosperm-like related traits under increased temperature and intense droughts. Our results show functional composition changes over relatively short time scales in European forests. These changes are largely determined by tree mortality, which should be further investigated and modelled to adequately predict the impacts of climate change on forest function.

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 to climatic extremes have led to changes in tree demography (Allen *et al.*, 2015), forest productivity (Ruiz-Benito *et al.*, 2014b) and carbon cycle (Frank *et al.*, 2015). There is a long tradition of studies analysing how functional traits change along climatic gradients (Díaz *et al.*, 2016). However, few studies have investigated how temporal changes in functional trait distributions are driven by changing climatic conditions and quantified potential changes in functional composition (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). Ongoing climate change –particularly intense droughts and increased temperatures– have already translated into increased tree mortality (Allen *et al.*, 2015), which may lead to latitudinal and altitudinal changes in forest species distribution (e.g. Benito-Garzón *et al.*, 2013, Urli *et al.*, 2014). 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). 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). Importantly, co-variation between traits implies that functional strategies can be described using a few axes of trait variation (Westoby, 1998, Westoby *et al.*, 2002). In general, angiosperm and gymnosperm species have contrasting functional traits that can be linked to their different life history strategies and responses 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. Although differences in drought-induced mortality have been found for functional trait values of dominant species, differences in mortality are not so easily identifiable using taxonomic or functional groups (e.g. angiosperms vs. gymnosperm, Anderegg *et al.*, 2016, Greenwood *et al.*, 2016).

Here, we quantified recent changes in forest functional composition by investigating 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 recent 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) covering the large latitudinal gradient of Europe (*c*. 5.000 km). For each tree we compiled information on the species identity (see Table S1), 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. S1). 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 are distributed from boreal to temperate and Sub-Mediterranean biomes, see Table 1). We used this classification because we expected angiosperm and gymnosperm forests –showing distinct patterns of leaf type: broad-leaved deciduous or needle-leaved evergreen, respectively– 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 specifically 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. S1).

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 compiled five traits which were available for c. 95% of the species (see Table S1): 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 S1). We quantified changes in functional composition as the absolute annual change in each functional trait selected instead of a relative change, because it informs well about both the direction of the change and its magnitude (i.e. positive or negative, and the absolute value of the change, Fig. S1 and Fig. S2).

Potential drivers of changes in forest functional composition

Each forest inventory plot was characterised by climate, stand development and demographic rate variables (see Fig. S3). 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 of the three components that were not strongly correlated with each other 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 the change in functional composition of European forests for each trait separately. As there were strong correlations in the absolute changes in different functional traits (Fig. S4) we explored the relationship between the functional traits using a Principal Component Analyses (R Core Team, 2015). We selected 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 (Fig. 1). 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, as these models allow accommodating complex, direct and indirect relationships between variables that go beyond the simple distinction between explanatory and response variables. The two latter analyses are explained in more detail in the following sub-sections, and were repeated including only those plots with no record of recent management to check for deviations of the patterns observed from models parameterised using all plots (Appendix S3).

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

We modelled 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. S1 and Fig. S3). 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). Forest type was included as an interaction with all potential fixed effects. All the numerical variables were examined for outliers and departures from normality; standardised (i.e. the mean was subtracted from 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 compared the full model with candidate models in which each of the interactions and then each interaction and main effect were removed. We selected the most complex model that reduced AIC by more than 2 units from the next simplest model (Hilborn & Mangel, 1997, Burnham & Anderson, 2002). As an indication of relative variable importance, we report the increase in AIC produced by removing each main effect and interaction included in the most parsimonious model. The relative importance of each predictor variable was also calculated as the sum of Akaike weight values of the models that contained that variable from all the potential set of models (i.e. values close to 1 indicate high importance, Burnham & Anderson, 2002). 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-R^2 (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 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 type 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) and Akaike weights were calculated using MuMIn library (Barton, 2016) in R version 3.2.2. (R Core Team, 2015).

Demographic drivers of changes in functional composition

We conducted piecewise structural equation modelling 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 forest development (see hypotheses in Fig. 2 and Appendix S2 for more details). Piecewise SEM combines information from multiple separate linear models into a single causal network and allowed us to incorporate random structures (Shipley, 2009). We used as endogenous variables (i.e. response variables in the separate linear models): (i) forest development, i.e. mean d.b.h. (mm), tree density (No. trees ha^{-1}), and functional diversity; (ii) demography, i.e. tree growth (log, cm^{2} ha^{-1} yr^{-1}) and tree mortality (log +0.01, cm^{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 scores of the changes in the five functional traits.

Firstly, we performed a multilevel path analysis (see Appendix S2) for the entire dataset, including all forest types, which allowed us to detect general trends in the changes in functional composition related to demography, climate, stand structure and diversity. Pseudo-R^{2} (proportion of variance explained in the model by both the fixed and random factors) was used to provide an estimation of variance explained (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 each of the five functional traits. Our exploratory analysis indicated shifts to both positive and negative values for all five traits (i.e. towards larger and smaller absolute values, respectively, Fig. S1 and 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 (PC1, explaining 50% of the variance) was strongly and negatively correlated with changes in leaf mass per area, and strongly and positively correlated with changes in wood density (Fig. 1 and Fig. S4). These functional traits are partially associated with functional strategies that distinguish between angiosperms and gymnosperms: positive values of PC1 reflect a greater dominance of angiosperm-like strategies (i.e. higher wood density and lower leaf mass per area, and higher vulnerability to xylem embolism and seed mass), whereas negative values reflect a greater dominance of gymnosperm-like strategies (i.e. lower wood density and greater leaf mass per area, see Fig. 1 and Appendix S4). Because of this association, we compared how the changes in PC1 (hereafter, trait-based approach) correlated with changes in the proportion of gymnosperms (hereafter, taxonomic-based approach). Although the relationship was linear (see Appendix S4) the correlation was relatively low ($r < 0.4$), indicating that changes in functional composition along the PC1 axis may not always correspond to a change in the proportion of gymnosperms. We also performed the linear models and the path analyses for the changes in the proportion of gymnosperms as shown in Appendix S4, allowing us to compare trait-based results with taxonomic-based results. The second axis of the PCA (PC2, explaining 20% of the variance) was highly and negatively correlated with changes in maximum tree height (Fig. 1 and Fig. S4). Therefore, 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 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

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 1). The best 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. S6 and Fig. S7 and standardised parameter values in Table S2). In the best model predicting PC1, the inclusion of variables related to recent climate change was supported, but their importance was lower than for forest development (see drop in ΔAIC in Table 2 when temperature anomalies and intense droughts were removed from the model). In the best model predicting PC2, functional diversity and water availability were the most strongly supported variables (Table 2).

Figures 3 and 4 represent the predicted changes in functional composition measured through PC1 and PC2, respectively, for each forest type (see density plots in Fig. S8 and relative changes in PC1 in Fig. S9) along gradients of climate (i.e. water availability, temperature anomaly and drought) and stand development (i.e. density, mean d.b.h. and diversity). The graphics have been coloured to reflect the magnitude and direction of the change along the PCA axes. PC1 is related to shifts in functional trait values towards a lower wood density and higher leaf mass per area (corresponding to the blue colour in Fig. 3 which reflects positive changes in PC1) or the contrary (red colour in Fig. 3, which reflects negative changes in PC1). PC2 was related to changes in maximum tree height (brown colour in Fig. 4 reflects a decrease in maximum tree height). The patterns of change predicted using PC1 and PC2 along climate and stand development gradients, based only on those plots with no record of recent management, were generally consistent with those observed for all plots (see Appendix S3).

In broad-leaved deciduous forests greater shifts towards lower wood density and larger leaf mass per area (corresponding to red colours in Fig. 3a) occurred where low water availability (more negative WAI values) coincided with medium-high tree density or mean d.b.h. (i.e. larger than 300 trees ha^{-1} and 200 mm, respectively), where low temperature anomalies coincided with low tree density (i.e. lower than 0.2 ºC and 500 trees ha^{-1}, respectively), and in plots with high functional diversity or under intense droughts (i.e. SPEI values < -2). At high water availability (WAI > 50%) the models predicted little change in the functional composition across the entire range of mean diameter and stand densities (Fig. 3a). In needle-leaved evergreen forests the greatest shifts towards greater wood density and lower leaf mass per area (corresponding to blue colours in Fig. 3c) occurred in plots with low functional diversity (FD < 0.10), small mean diameter and high water availability and temperature anomalies (i.e. mean d.b.h. < 200 mm and WAI > 0 or TA > 0.2 ºC). In the case of Mediterranean forests, we found similar patterns for broad- and needle-leaved species. Changes towards a stronger dominance of individuals with greater wood density and lower leaf mass per area in Mediterranean forests (i.e. blue colours in Fig. 3b,d) were observed at high water availability, high temperature anomalies and relatively mild droughts (specially WAI > 0 %, TA > 0.5 ºC, and minimum SPEI > -1.5), with higher intensity when tree density and mean tree diameters are large. 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 species dominated by lower wood density and greater leaf mass per area at low water availability irrespective of tree density, whereas this pattern was not clear in Mediterranean coniferous forests. The analysis performed on the change in the proportion of gymnosperms confirmed that most patterns in wood density and leaf mass per area strongly corresponded to changes between angiosperm and gymnosperm-dominated stands, but some notable differences were found (see detailed results in Appendix S4). Particularly, shifts towards a functional group that is different to the dominant group were more apparent along climatic gradients in the taxonomic-based analysis, especially of increasing drought (see Fig. S4.4 in Appendix S4).

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

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. 5), although the ability of the underlying linear models to explain growth was greater than for mortality models (see R^2 for growth and mortality models = 0.58, 0.41, respectively; Fig. 5). 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, similar to the observed changes in the proportion of gymnosperms and plots with no evidence of recent management (see Appendix S3 and S4). For PC2 the mortality effect was negative and the magnitude was less strong, which reflected a weak increase 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 Appendix S2). The strongest effect of mortality on PC1 and PC2 was found in Mediterranean conifers (see magnitude of standardised parameters in Appendix S2).

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. 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).

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

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 density 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). Although the change in functional composition using PC1 axis corresponds partially to a taxonomic change towards a greater proportion of gymnosperms (Appendix S4), our trait-based approach allowed us to further understand the conserved patterns given the substantial overlap of trait values across communities between and within functional groups. This is consistent with recent meta-analyses showing that trait-based approaches are able to better identify drought-induced tree mortality patterns than taxonomic-based approaches (Anderegg et al. 2016; Greenwood et al. 2016). 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).

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

We observed that 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, and the corresponding changes in tree density, size and diversity. In relatively well-developed mature forests (i.e. tree densities and mean tree diameter larger than 500 trees ha^{-1} and 200 mm, respectively) with temperature anomalies higher than 0.2 ºC we found a change towards a greater proportion of individuals with high wood densities and low leaf mass per area in broadleaved forests and Mediterranean conifers. Our observation that gymnosperms could be vulnerable to increases in temperature and water stress is consistent with recent studies that reported or predicted high mortality in conifers (McDowell and Allen, 2015, 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). Recent meta-analyses did not find clear differences between angiosperm and gymnosperm mortality responses to drought, despite clear trait-level differences in specific leaf area, wood density or hydraulic traits (Anderegg *et al.*, 2016; Greenwood *et al.*, 2016). However, we cannot discount the possibility that the observed functional changes towards a greater proportion of angiosperm-like 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). In fact, the observed increase in the proportion of angiosperms might 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).

Intense droughts led to changes towards functional traits values different from the dominant group in all forest types with mean tree diameter < 400 mm, and this was even more distinct when assessed as changes in the proportion of gymnosperms (Appendix S4). Furthermore, this change was not observed in conifers of small-medium diameter (i.e. mean d.b.h. < 400 mm) and at low diversity (Fig. 3). The shift in the dominant functional strategy in broad-leaved evergreen forests under intense droughts at large diameters is in accordance with previous studies that suggest trade-offs between plant size and drought tolerance (i.e. Ryan *et al.*, 2006, Moles *et al.*, 2009, Bennett *et al.*, 2015). This change towards traits linked to gymnosperm-like strategies 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 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 composition linked to leaf mass per area and wood density, and corresponding functional strategies (i.e. changes in PC1 and proportion of gymnosperms, respectively) across Europe were strongly dependent on functional diversity. The influence of diversity was strong when compared to climatic variables, leading to clear patterns of change in all forest types (Fig. 3). Areas of low tree diversity and monospecific forests might correspond with planted-forests, which in many cases are planted outside their natural climatic range even when they are composed of native species (e.g. Ruiz-Benito et al. 2012). At high diversity levels in Mediterranean forests, we found greater shifts towards a larger dominance of individuals with greater wood density, lower leaf mass per area and, overall, angiosperm-like strategies. In contrast, diverse temperate and boreal forests tended to change towards a larger dominance of greater leaf mass per area, lower wood density and gymnosperm-like strategies. The trends predicted with increasing functional diversity are consistent with the expectations of the secondary successional trajectory expected in the different forest types or regions, 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 in 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. S1 and S3) 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. 3), 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 species with low wood density and high leaf mass per area, suggesting increased growth of fast-growing strategies (i.e. gymnosperm-like strategies) and higher mortality of slow-growing strategies (i.e. angiosperm-like strategies, Fig. 3a,b and Appendix S4). At the rear edge of broad-leaved temperate forests (i.e. generally related to low water availability) an altered demography, with 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).

Many of the changes along climatic and forest development gradients were related to increases in maximum tree height (see green colours in Fig. 4). 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 (see also Marks *et al.*, 2016), which might be reflecting the expected secondary succession trajectory. In wet sites (i.e. water availability > 0), we found that Mediterranean conifer forests (i.e. maximum height *c.* 28 m, see Fig. S10) 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*; with maximum tree height of *c.* 41 m, (Rivas-Martínez, 1987, Costa *et al.*, 1997). 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. with maximum height of *c.* 19 m for *Q. ilex* and *Q. suber*; and *c.* 24 m for *Q. faginea* and *Q. pyrenaica*, see Fig. S10). 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 when compared to tree growth 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). Due to limitations combining data from different inventories we focused on adult trees with d.b.h. > 10 cm, but we acknowledge that tree regeneration plays a key role in long-term forest dynamics and it could be highly vulnerable to climate change effects (e.g. Zhu *et al.*, 2012). Furthermore, we are working with permanent forest plots along the entire European continent in which we could not analyse the effect of other global change drivers –e.g. land use change, nitrogen deposition or extreme fires, storms or droughts– that might further drive changes in forest structure and composition beyond certain thresholds (e.g. Frank *et al.*, 2015; Jump *et al.*, 2016). However, we have identified tree mortality as a key driver of three patterns of change in the functional strategies observed across European forests. Firstly, increased mortality of species with low wood density and high leaf mass per area (see also Greenwood *et al.*, 2016, McDowell and Allen, 2015) could be driving changes towards a greater dominance of angiosperm-like functional traits across Europe particularly under high temperature anomalies in all forest types and under intense droughts in mature needle-leaved forests. Secondly, 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). Finally, the change towards a larger proportion of angiosperms in Mediterranean forests with tree densities and mean diameter larger than 500 trees ha^{-1} and 200 mm, respectively, and not strongly limited by water availability, agrees with the greater role of mortality relative to growth in forests 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 functional composition in European forests can be characterised along two axes of variation summarising leaf-wood traits, on the one hand, and maximum height on the other. 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 conclude 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. 5). Our study suggests that climatic and forest developmental interactions are critical to adequately predict forest functional responses under climate change (van Bodegom *et al.*, 2014). Further studies are essential in order to better understand drivers of tree mortality and link changes in plant functional traits to ecosystem functioning (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.

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

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

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

Table S1 Trait data used in the study.

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

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

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

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

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

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

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

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

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

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

Fig. S10 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)	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)	*	*

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 (see Appendix S4).

Table 2 Comparisons of alternate models based on Akaike Information Criterion (AIC) to test pair-wise interactions and main effects 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. Relative importance of variables was also tested using 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 × TD	9	13	No ID	89	172	ID	1.00	1.00
No TA × TD	21	18	No dm	382	434	dm	1.00	1.00
No ID × TD	2	19	No WAI	486	1495	WAI	1.00	1.00
No WAI × d_m	32	91	No TA	589	240	TA	1.00	1.00
No TA × d_m	64	16	No TD	802	113	TD	1.00	1.00
No ID × d_m	34	68	No FD	952	1619	FD	1.00	1.00
No WAI × FD	148	510	AIC	230286	174982			
No TA × FD	385	49	R^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 (WAI), temperature anomaly (TA), intense drought (ID), tree density (TD), mean d.b.h. (d_m) and functional diversity (FD), and (a) all interactions tested, and (b) all interactions supported by the best model in (a). The best fitting model (the full model in our case) is given a ΔAIC value of zero (bold). This model is compared with models in which the effect of the individual predictor variables (considering the main effects and/or the interactions) has been removed. 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 R2 for the best models are also shown.

FIGURE LEGENDS

Figure 1. 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 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. 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 lower LMA and higher WD, while red colour represents changes towards lower WD and higher LMA. The variables vary between the observed 99% percentiles in each forest type. Convex hull lines covering the presence of data points in each panel are represented using black lines and density plots are shown in Fig. S8.

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

Figure 4. 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. The variables vary between the observed 99% percentiles in each forest type. Convex hull lines covering the presence of data points in each panel are represented using black lines sand density plots are shown in Fig. S8.

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

Figure 5. 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. $P \geq 0.05$ of the estimated parameter in Appendix S2). The estimated coefficient for the effects of mortality and growth is provided next to the arrow and the thickness of the significant paths has been scaled based on the magnitude of the standardised regression coefficient. The conditional R^2 of the models (i.e. based on the variance of both the fixed and random effects) is provided in in the boxes of response variables.