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RESEARCH PAPER

Functional diversity underlies demographic responses to environmental variation in European forests

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ABSTRACT

Aim Biodiversity loss and climate-driven ecosystem modification are leading to substantial changes in forest structure and function. However, the effects of diversity on demographic responses to the environment are poorly understood. We tested the diversity hypothesis (measured through functional diversity) and the mass ratio hypothesis (measured through functional identity) in relation to tree growth, tree mortality and sapling abundance. We sought to determine whether functional diversity underlies demographic responses to environmental variation in European forests.

Location Europe (Spain, Germany, Wallonia, Finland and Sweden).

Methods We used data from five European national forest inventories from boreal to Mediterranean biomes (*c.* 700,000 trees in 54,000 plots and 143 tree species) and the main forest types across Europe (i.e. from needle-leaved evergreen forests to broad-leaved deciduous forests). For each forest type, we applied maximum likelihood techniques to quantify the relative importance of stand structure, climate and diversity (i.e. functional diversity and functional identity) as determinants of growth, mortality and sapling abundance. We also tested whether demographic responses to environmental conditions (including stand density, evapotranspiration and temperature anomalies) varied with functional diversity.

Results Our results suggest that functional diversity has a positive effect on sapling abundance and growth rates in forests across Europe, while no effect was observed on tree mortality. Functional identity has a strong effect on mortality and sapling abundance, with greater mortality rates in forests dominated by needle-leaved individuals and a greater abundance of saplings in forests dominated by broad-leaved individuals. Furthermore, we observed that functional diversity modified the effects of stand density on demographic responses in Mediterranean forests and the influence of evapotranspiration and temperature anomalies in forests widely distributed across Europe.

Main conclusion Our results suggest that functional diversity may play a key role in forest dynamics through complementarity mechanisms, as well as by modulating demographic responses to environmental variation.

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Keywords

Boreal biome, climate warming, forest succession, FunDivEUROPE, growth, Mediterranean biome, mortality, plant functional traits, recruitment, temperate biome.

INTRODUCTION

Forests provide multiple ecosystem functions and services fundamental to human well-being (e.g. Gamfeldt *et al.*, 2013). However, forests are complex ecosystems dominated by long-lived species of large size and often limited dispersal ability that face major challenges due to loss of diversity and rapid climate change (e.g. Jump & Peñuelas, 2005). Diversity loss is leading to important changes in the functioning of multiple ecosystems, similar in magnitude to other drivers of global change (e.g. Tilman *et al.*, 2012). In addition, climate change is altering the basic demographic responses of tree species, from increases in drought-induced tree mortality events to reductions in recruitment and growth (e.g. Settelle *et al.*, 2014; Allen *et al.*, 2015).

Two main hypotheses have been proposed to explain the underlying influence of plant functional traits on forest functioning: (1) the diversity hypothesis, which states that functionally different species can coexist due to complementarity mechanisms that can lead to higher levels of forest functioning; and (2) Grime's mass ratio hypothesis, which states that the functional traits of dominant species in a community have most influence on the level of ecosystem functioning (e.g. Grime, 1998; Mokany *et al.*, 2008). Most biodiversity and ecosystem functioning studies in forests have focused on tree growth (e.g. Morin *et al.*, 2011; Ruiz-Benito *et al.*, 2014a). However, Liang *et al.* (2007) observed that diversity effects could be even larger for recruitment than for growth in conifer forests. In addition, Lasky *et al.* (2014) found that the magnitude of the effects of diversity on biomass changes was larger in early successional than late-successional tropical forests, due to differences in mortality and growth patterns between the stages. Despite growing evidence of effects of functional diversity and identity on tree growth in forests from boreal to Mediterranean climates, it is not clear whether the effects of diversity are as important for other demographic processes such as recruitment and mortality. Furthermore, there is increasing evidence that the effects of diversity on growth may be modulated by other factors such as climatic conditions (Jucker *et al.*, 2015; Toïgo *et al.*, 2015).

Recent climate change includes temperature increases (e.g. warmer summers in the Mediterranean and warmer winters in boreal regions) and more frequent and intense droughts that are leading to mortality events (Allen *et al.*, 2015) and reductions in recruitment (Walck *et al.*, 2011). Interactions between climate and stand structure are altering demographic patterns and decreasing the rate of biomass accumulation in ecosystems with low water availability (Ruiz-Benito *et al.*, 2014b). The alteration in demographic responses may result in changes to the distributional range of species under climate change (e.g. Benito-Garzón *et al.*, 2013). Mortality responses to climate have been shown to largely depend on stand structure (Ruiz-Benito *et al.*, 2013), meanwhile recruitment patterns are essential determinants of future community composition and structure (Carnicer *et al.*, 2014). During the last decade there has been intense debate over the importance of the effects of diversity on forest functioning, yet these studies have mainly focused on species richness and tree growth as a key ecosystem function (e.g. Zhang *et al.*, 2012; Vilà *et al.*, 2013). Two recent studies suggest that complementarity mechanisms in forest functioning could be more important in resource-limited forests such as drought-prone forests in the Mediterranean (Grossiord *et al.*, 2014b; Jucker *et al.*, 2015). However, the potential effect of diversity on multiple demographic responses to abiotic and biotic environment remains poorly understood.

We used five national forest inventories (NFIs) with more than 55,000 plots covering Mediterranean to temperate and boreal biomes, and including the main forest types across Europe (i.e. broad-leaved versus needle-leaved and evergreen versus deciduous forests; see Fig. 1 and Baeten *et al.*, 2013). We collated data on four key traits for plant performance for the 143 species (i.e. leaf mass per area, wood density, maximum tree height and seed mass; e.g. Díaz *et al.*, 2016) and tested the influence of functional composition on demography, following: (1) the diversity hypothesis, i.e. functional diversity determines growth and recruitment through complementarity mechanisms (particularly in water-limited Mediterranean forests) and ameliorates the negative effects of environment (i.e. including competition, climate and recent climate warming) on demography; and (2) the mass ratio hypothesis, i.e. functional identity influences demographic patterns due to the dominance of certain functional traits through selection mechanisms, particularly between contrasting life-history strategies. To test these hypotheses, we quantified the functional composition of each plot as the absolute effect of functional diversity (FD; measured as the dispersion of key traits in each plot) and functional identity (FI; measured as the community-weighted mean of a single trait in

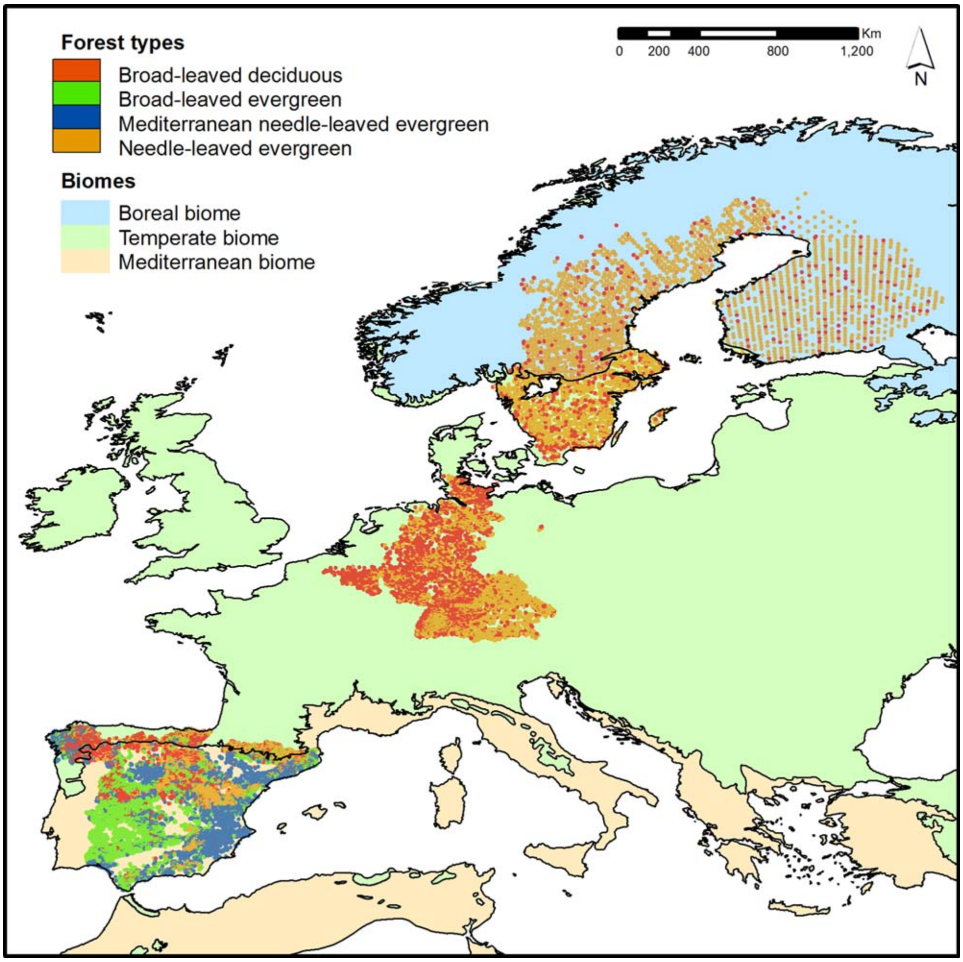

Figure 1 Spatial distribution of the national forest inventory plots for the forest types used in this study and the underlying biome distribution (modified from Olson *et al.*, 2001).

each plot) on growth, mortality and sapling abundance. Secondly, we explored whether demographic responses to biotic and abiotic environmental conditions (i.e. including competition, climate and recent temperature increases) were modified by functional diversity.

METHODS

Forest inventory dataset and demographic variables

We compiled data from the NFIs of Spain, Germany, Belgium (Wallonia), Sweden and Finland (see Appendix S1 and Table S1 in Supporting Information). For each tree we compiled information regarding the species name (see Table S2), diameter at breast height (d.b.h., mm) and status (alive or dead). We classified each plot based on the abundance of the species in the following classifications: (1) leaf characteristics (i.e. broad-leaved versus needle-leaved, deciduous versus evergreen), and (2) Mediterranean distribution (i.e. distributed only in areas with a Mediterranean climate; see Table S1), because the response to climate and, therefore, the strength of diversity effects may be different in forests that are well adapted to extreme climatic conditions (Grossiord *et al.*, 2014a,b). We only considered forest types with more than 1000 plots, resulting in 52,180 plots in the following forest types: broad-leaved deciduous, Mediterranean broad-leaved evergreen, Mediterranean needle-leaved evergreen forests and other needle-leaved evergreen forests (Fig. 1, Table 1).

As demographic variables we used (see also Appendix S2): (1) tree growth (cm^2 ha^{-1} $year^{-1}$) calculated as the annual sum of the basal area increment of adult trees that survived both censuses and new adult trees in the second census (i.e. d.b.h. $>$ 10 cm and height $>$ 130 cm); (2) tree mortality (cm^2 ha^{-1} $year^{-1}$) calculated as the annual basal area of adult trees lost between consecutive inventories; and (3) sapling abundance (no. of saplings ha^{-1}) calculated as the abundance of individuals with a height between 30 and 130 cm in the second census of the consecutive inventories (see Table S1, Fig. S1).

Abiotic and biotic determinants of demographic responses

Initially, we selected 27 potential climatic variables based on temperature and precipitation which describe: (1) the spatial climatic variability over the period 1950–2000 (WorldClim, CGIAR-CSI GeoPortal and SPEIbase v2.2.; see the list of data sources in Appendix 1 and Table S3); and (2) recent climate change (NOAA, Boulder, CO, USA) defined as the differences in temperature or precipitation between the study period (i.e. the number of years between the two consecutive inventories plus 2 years before the first survey) and the mean value for the reference period (1900–2010).

Stand structure (i.e. stand tree density calculated as the number of trees per hectare, and mean d.b.h. calculated as the mean diameter of all trees in the stand) and community functional composition (i.e. FD and FI) were also estimated for each plot. We used four key traits to describe the functional composition (see Table S4; a list of sources for the trait data used can be found in Appendix 1): maximum tree height (m), wood density (g cm^{-3}), seed mass (mg) and leaf mass per area (g m^{-2}). These traits are widely recognized as key traits of plant function and performance: maximum height, wood density and seed mass are closely related to life-history strategy while leaf mass per area is related to resource acquisition and plant growth strategy (e.g. Paquette & Messier, 2011; Swenson *et al.*, 2012). FD (Laliberté & Legendre, 2010) was calculated as the dispersion of functional traits in each plot based on all traits and only seed mass, wood density and maximum height (see Appendix S2). FI (Lavorel *et al.*, 2008) was calculated as the community-level weighted mean of each trait in each plot.

Prior to parameterizing our maximum likelihood models of demographic responses, we performed variable selection from the available climatic and biotic variables (Figs S2 & S3). To select from the large climatic dataset we performed a principal components analysis (PCA) and selected potential evapotranspiration (PET, mm) as representative of spatial climatic variability (highly and negatively correlated with the first axis of the PCA, explaining 49.9% of the variance) and temperature anomaly (TA, °C) as representative of recent climate change (TA showed a stronger negative correlation with the first axis of the PCA than precipitation anomaly). To represent stand structure, we selected tree density (no. of trees ha^{-1}) and mean tree diameter (size, mm) to account for stand density and developmental stage. We selected FD based on seed mass, wood density and maximum height, and FI based on leaf mass per area (hereafter $\mathrm{FI_{LMA}}$). The FD index was selected because the correlation between all diversity indices was high (i.e. considering all traits or subset of traits, $r > 0.85$) and the subset of traits including seed mass, wood density and maximum tree height has been previously identified as a good predictor of forest functioning (the same indices were used in Paquette & Messier, 2011; Ruiz-Benito *et al.*, 2014a) and competitive outcomes (Kunstler *et al.*, 2016). The FI index selected was based on leaf mass per area and has been identified as a good indicator of contrasting life-history strategies and it is different for the dominant species in the forest types (see Fig. S3; e.g. Wright *et al.*, 2004).

Maximum likelihood analysis of tree growth, tree mortality and sapling abundance

We fitted nonlinear models for tree growth (cm^2 ha^{-1} year^{-1}), tree mortality (cm^2 ha^{-1} year^{-1}) and abundance of saplings (no. of saplings ha^{-1}) for each forest type separately. The predicted demographic responses (μ_i) were modelled using the following nonlinear model:

$$\mu_i = \mu_{\mathrm{pot}} \times \text{climate effect} \times \text{structural effect} \times \text{functional composition effect} \tag{1}$$

where $\mu_{\mathrm{pot}}\mu_{\mathrm{pot}}\ \mu_{\mathrm{pot}}$ is an estimated model parameter that represents the maximum potential value of tree growth, tree mortality or sapling abundance when all the predictors are at their optimal values; i.e. the potential predictor are sets of nonlinear terms that contain scalar modifiers ranging from 0 to 1 that quantify the influence of (1) climatic conditions (i.e. 'climate effect': PET and TA, see equation 2); (2) stand structure (i.e. 'structural effect': density and size, defined in equation 3); and (3) functional composition (i.e. 'functional composition effect': FD and $\mathrm{FI_{LMA}}$, defined in equation 4).

For the climate and structural effects, we selected a Gaussian function because it is flexible enough to allow for typical hump-shaped species–environment relationships, but also allows for monotonic or sigmoidal responses within restricted ranges of either axis (Gómez-Aparicio *et al.*, 2011; Ruiz-Benito *et al.*, 2014a). Thus, the climate effect on demographic responses was modelled using a Gaussian functional of the form:

$$\text{Climate effect} = \exp\left[-\frac{1}{2}\left(\frac{\mathrm{PET} - \mathrm{XPET_a}}{\mathrm{XPET_b}}\right)^2\right] \times \exp\left[-\frac{1}{2}\left(\frac{\mathrm{TA} - \mathrm{XTA_a}}{\mathrm{XTA_b}}\right)^2\right] \tag{2}$$

where the parameters $\mathrm{XPET_a}$ and $\mathrm{XTA_a}$ represent the PET and TA at which maximum tree growth occurs, and $\mathrm{XPET_b}$ and $\mathrm{XTA_b}$ are the parameters that control the variance of the normal distribution (i.e. the breadth of the function). The structural effect on demographic responses was modelled using a bivariate Gaussian function:

$$\text{Structural effect} = \exp\left[-\frac{1}{2}\left(\frac{\mathrm{Density} - \mathrm{XSTD_a}}{\mathrm{XSTD_b}}\right)^2\right] \times \exp\left[-\frac{1}{2}\left(\frac{\mathrm{Size} - \mathrm{XS_a}}{\mathrm{XS_b}}\right)^2\right] \tag{3}$$

where the density effect is measured in terms of stand tree density (no. of trees ha^{-1}) and the size effect is measured through stand mean d.b.h. (mm). $\mathrm{XSTD_a}$ and $\mathrm{XS_a}$ are the density and size, at which maximum growth occurs, and $\mathrm{XSTD_b}$ and $\mathrm{XS_b}$ are the estimated parameters that control the breadth of the function.

For tree growth and sapling abundance, the influence of FD was modelled using a variation of the exponential form, because FD can have a positive effect on demographic responses at low values of FD but can later reach an asymptotic level (e.g. Paquette and Messier, 2011; Ruiz-Benito *et al.*, 2014a). Functional identity ($\mathrm{FI_{LMA}}$) was modelled using a Gaussian function because it is flexible enough to allow for the quadratic and monotonic responses of forest performance along FI gradients (e.g. Ruiz-Benito *et al.*, 2014a). Thus, the 'community functional composition effect' was modelled following the next functional form:

$$\text{Functional composition effect} = 1 - [\exp(\text{XFD}_a \times \text{FD}) - \text{XFD}_b] \times \exp\left[-\frac{1}{2}\left(\frac{\text{FI}_{\text{LMA}} - \text{XFI}_a}{\text{XFI}_b}\right)^2\right] \quad (4)$$

where the parameter XFD_a determines the shape of the effect of FD on the predicted variable and XFD_b defines the intercept of the function. The parameter XFI_a represents the FI_{LMA} value at which maximum tree growth and sapling abundance occurs, and XFI_b determines the breadth of the function. For stand mortality, we considered that FD could reduce mortality rates and, thus, we used a variant of equation 4 where the FD was in this case modelled using a negative exponential form:

$$\text{Functional composition effect} = [\exp(\text{XFD}_a \times \text{FD}) - \text{XFD}_b] \times \exp\left[-\frac{1}{2}\left(\frac{\text{FI}_{\text{LMA}} - \text{XFI}_a}{\text{XFI}_b}\right)^2\right] \quad (5)$$

where the parameter XFD_a determines the shape of the effect of FD on the predicted variable and XFD_b defines the intercept of the function.

The indirect effects of FD on the demographic responses to environmental conditions were tested through variants of X_b parameters in equations 2 and 3. We therefore modified the expression that was used to obtain the fitted X_b parameters that control the breadth of the function and, therefore, determine the strength of the environmental effect on demography. The X_b parameters which determine the strength of the environmental effect on demography (i.e. XSTD_b, XPET_b and XTA_b; relating to the effects of density, PET and TA, respectively, on demographic responses) were allowed to vary as a function of functional diversity following:

$$X_b = \beta \times \text{FD} + X_b' \quad (6)$$

where β is a parameter that indicates how FD modifies demographic responses to the environment. $\beta = 0$ reflects no influence of FD on demographic responses to environmental conditions. As we hypothesized larger demographic responses to the environment when FD is low, $\beta > 0$ was allowed for tree growth and sapling abundance and $\beta < 0$ was allowed for tree mortality (i.e. at high FD there is a reduced influence of density, PET and/or TA on tree growth, tree mortality and/or sapling abundance responses).

Parameter estimation, model selection and validation

We fitted separate nonlinear models of tree growth, tree mortality and sapling abundance for each forest type. To select the best model, we followed the principle of parsimony and used a two-unit difference in the Akaike information criterion (AIC) as a support interval to assess the strength of evidence of individual maximum likelihood parameter estimates, being roughly equivalent to the 95% support limit defined using a likelihood ratio test (Burnham & Anderson, 2002). Thus, the full model was compared with models that ignored the effect of each predictor variable (i.e. not including the effect of PET, TA, density, size, FD and FI_{LMA}, respectively, in each model) which also informed on the strength of the evidence for including each variable in the final model.

Given the high number of zeros in the tree mortality and sapling abundance data (see Table 1), a zero-inflated normal distribution (ZIN) and a negative binomial distribution were used, respectively, while a normal error distribution was used for tree growth (see Fig. S5). For tree mortality our statistical model estimates two components simultaneously: (1) the probability of mortality based on the binomial variable related to stand mortality, and (2) the predicted basal area lost due to mortality in the plots that experienced mortality. The ZIN function has the following functional form:

$$\text{prob}(Y = y_i) = \begin{cases} p_s \text{ if } y_i = 0 \\ (1 - p_s)\,\text{normal}\,(y_i|\theta) \text{ if } y_i > 0 \end{cases} \quad (7)$$

where y_i represents the basal area lost due to natural mortality in plot i and p_s represents a constant probability across the data set of getting zero mortality. When $y_i > 0$, stand mortality was modelled using a normal distribution given the data y_i and the parameters θ, obtained from structural, climatic and diversity effects following equations 1–5.

The parameter estimates provide the basis for determining the magnitude of the influence of a given process, with maximum likelihood estimates of parameter values close to zero or confidence intervals overlapping zero indicating no effect. We used simulated annealing optimization procedures to determine the parameters that maximize the log-likelihood of observing tree growth, mortality and recruitment (Goffe *et al.*, 1994). As a measure of the goodness of fit we calculated the R^2 of the nonlinear models fitted (1 – SSE/SST; where SSE is the sum of squares error and SST the sum of squares total). As a measure of bias in the prediction we plotted the observed and predicted data and calculated the slope of the regression with a zero intercept, where an unbiased model should have a slope of regression equal to one (i.e. line 1:1). In addition, we checked the influence of census interval using similar approaches to Chen & Luo (2015) (see Appendix S2). The analyses were performed using the likelihood package 1.6 (Murphy, 2012) in R.2.15 (R Core Team, 2012).

RESULTS

Influence of climate and structural and functional composition on tree growth

The most parsimonious models for tree growth in Mediterranean evergreen forests (both needle- and broad-leaved forests) included variables related to climate, stand structure and

Table 1 Mean and 99% percentiles [min., max.] of tree growth (Growth), tree mortality (Mortality), sapling abundance, stand tree density (Density), mean d.b.h., potential evapotranspiration, absolute temperature anomaly, functional diversity (adimensional) and functional identity based on leaf mass per area for each forest type.

	Broad-leaved deciduous	Mediterranean broad-leaved evergreen	Mediterranean needle-leaved evergreen	Other needle-leaved evergreen
Growth (cm^2 ha^{-1} year^{-1})	40.99 [0.73, 172.41]	13.63 [0.3, 129.95]	36.04 [1.07, 154.17]	51.43 [0.53, 228.62]
Mortality (% zeros) (cm^2 ha^{-1} year^{-1})	7.86 (79.11%) [0, 153.82]	3.81 (86.58%) [0, 117.19]	16.97 (68.29%) [0, 245.32]	8.22 (80.82%) [0, 175.05]
Sapling abundance (% zeros) (no. saplings ha^{-1})	1509 (44.31%) [0, 21759]	1169 (31.03%) [0, 6629]	1018 (25.09%) [0, 6366]	1204 (48.59%) [0, 13512]
Density (no. trees ha^{-1})	393 [5, 2117]	184 [5, 1394]	310 [9, 1689]	487 [14, 2275]
Mean d.b.h. (mm)	282.5 [103, 902]	303.19 [102, 828]	238.73 [108, 547]	222.71 [103, 589]
Potential evapotranspiration (mm)	810 [438, 1229]	1107 [781, 1349]	1050 [771, 1310]	739 [432, 1134]
Temperature anomaly (°C)	0.4 [–0.07, 0.92]	0.53 [0.25, 0.87]	0.54 [0.28, 0.88]	0.44 [–0.25, 1]
Functional diversity	0.06 [0, 0.2]	0.03 [0, 0.25]	0.02 [0, 0.2]	0.04 [0, 0.2]
Functional identity leaf mass per area (g m^{-2})	84 [47, 185]	152 [107, 234]	286 [182, 412]	196 [84, 268]
No. of plots (% represented)	10,553 (19.42%)	9,490 (17.50%)	11,057 (20.39%)	21,080 (38.88%)
Composition (% represented)	*Fagus sylvatica*, *Quercus robur*, *Q. pyrenaica*, *Q. petraea*, *Castanea sativa*, *Q. faginea* (70%)	*Quercus ilex*, *Q. suber* (89.8%)	*Pinus halepensis*, *P. pinea*, *P. pinaster* (95%)	*Pinus sylvestris*, *P. nigra*, *Picea abies* (81%)

The number of plots and main species composition of each forest type (and percentage represented) is also given.

functional composition (Table 2). However, in forests broadly distributed throughout Europe functional composition was not strongly supported in the final model (i.e. broad-leaved deciduous and other needle-leaved forests; see ΔAIC in Table 2). The responses of tree growth to stand structure were stronger than those observed for climate (Table 2; see the largest increase in AIC when the effect of stand structure was dropped from the full models). All the models produced unbiased estimates of tree growth (i.e. slopes of predicted versus observed values were all close to one) and the explained variance (R^2) ranged from 43% for broad-leaved deciduous forests to 54% for other needle-leaved evergreen forests (Table 2).

FD and FI were particularly important determinants of tree growth in Mediterranean needle-leaved evergreen forests followed by Mediterranean broad-leaved evergreen forests (see Table 2). Tree growth increased slightly with FD in all forest types (Fig. 2a), and strongly with $\mathrm{FI}_{\mathrm{LMA}}$ in Mediterranean needle-leaved evergreen forests (Fig. 2b). FD also indirectly modified the responses of tree growth to stand density in Mediterranean forests (see Table 2, Fig. 3a) and to potential evapotranspiration in broad-leaved deciduous forests (Table 2 and Fig. 3b). Functionally diverse forests experienced lower effects on demography of the extremes of density or potential evapotranspiration.

Influence of climate and structural and functional composition on tree mortality

The final mortality models included variables related to climate (potential evapotranspiration and temperature anomalies), stand structure (i.e. stand basal area and mean d.b.h.) and FI (Table 2). The influence of stand structure on mortality was larger than that of climate and FI (see ΔAIC in Table 2). All of the models produced unbiased estimates of tree mortality and explained variance (R^2), ranging from 11% for broad-leaved deciduous forests to 34% for Mediterranean needle-leaved evergreen forests (Table 2).

Tree mortality was not influenced by FD (see $\Delta\mathrm{AIC} < 2$ when FD was removed from the full model in Table 2), whilst $\mathrm{FI}_{\mathrm{LMA}}$ had a strong influence, with a relative importance similar to that of potential evapotranspiration (Table 2). We observed maximum stand mortality towards high values of leaf mass per area (i.e. forests dominated by needle-leaved species; see Fig. 2c). Our results suggest that responses of mortality to environmental conditions could vary depending on FD in needle-leaved and broad-leaved deciduous forests (see β parameters in Table 2). The positive relationship between stand tree density and tree mortality was lower in more diverse Mediterranean needle-leaved forests (see Fig. 3c). Furthermore, FD reduced the influence of potential evapotranspiration on tree mortality in broad-leaved deciduous and other needle-leaved evergreen forests, and temperature anomalies in Mediterranean and other needle-leaved evergreen forests (Fig. 3a).

Influence of climate and structural and functional composition on sapling abundance

Climate variables were particularly important for determining patterns of sapling abundance in all forest types, followed by

Table 2 Comparisons of alternative models of tree growth (cm^2 ha^{-1} year^{-1}), tree mortality (cm^2 ha^{-1} year^{-1}) and sapling abundance (no. of saplings ha^{-1}) for the forest types studied using the Akaike information criterion (AIC).

	ΔAIC												
		Climate effect		Structural effect		Functional composition effect							
Response variable and forest type	Full*	No PET	No TA	No STD	No d_m	No FD	No FI_{LMA}	β_{PET}	β_{TA}	β_{STD}	R^2	Slope	NP
Tree growth:													
Broad-leaved deciduous	0	676	**220**	**2393**	**130**	**3**	0	**Y**	N	N	0.43	1.00	12
Mediterranean broad-leaved evergreen	0	**329**	**84**	**2549**	**82**	**811**	**3**	N	N	**Y**	0.53	1.00	14
Mediterranean needle-leaved evergreen	0	**182**	**3**	**4568**	**77**	**10**	**1566**	N	N	**Y**	0.54	1.00	14
Other needle-leaved evergreen	20	**3772**	**134**	**6769**	**57**	0	**19**	N	N	N	0.48	1.00	11
Tree mortality:													
Broad-leaved deciduous	1	**36**	**18**	**183**	**110**	0	**25**	**Y**	N	N	0.11	1.00	13
Mediterranean broad-leaved evergreen	0	**31**	**5**	**107**	**53**	1	**13**	N	N	N	0.34	1.00	12
Mediterranean needle-leaved evergreen	5	**5**	**21**	**871**	**374**	0	**42**	N	**Y**	**Y**	0.31	1.00	14
Other needle-leaved evergreen	0	**215**	**32**	**348**	**177**	0	**57**	N	**Y**	N	0.22	1.00	14
Sapling abundance:													
Broad-leaved deciduous	0	**48**	**26**	**4**	0	**4**	**55**	N	N	N	0.13	1.01	11
Mediterranean broad-leaved evergreen	3	**183**	0	**8**	**121**	**5**	**5**	N	N	N	0.25	1.00	11
Mediterranean needle-leaved evergreen	0	**145**	**22**	0	**9**	**30**	**30**	N	N	N	0.09	1.02	13
Other needle-leaved evergreen	0	**289**	**19**	**79**	**3**	**77**	**36**	**Y**	**Y**	N	0.14	1.01	15

The full models include the effects of potential evapotranspiration (PET, mm), temperature anomaly (TA, °C), stand tree density (STD, no. trees ha^{-1}), mean d.b.h. (d_m, mm), functional diversity (FD, adimensional) and functional identity based on leaf mass per area (FI_{LMA}, g m^{-2}). The 'No' models ignore the effect of the related explanatory variable. The final predictor variables included in each model are given in bold based on AIC comparison for the set of tree growth, tree mortality and sapling abundance models. AIC comparisons (ΔAIC_i) are shown for each set of models (i.e. tree growth, tree mortality or sapling abundance) through AIC differences of each model (AIC_i) with the model with minimum AIC (AIC_{min}): $\Delta AIC_i = AIC_i - AIC_{min}$. The best model is the one with $\Delta AIC_i = AIC_{min} = 0$. The β columns indicate whether (Y, yes; N, no) the best model included a term that allows evapotranspiration (β_{PET}), temperature anomaly (β_{TA}) or stand tree density (β_{STD}) to vary with functional diversity, changing the breath of the function (see equation 6). NP is the number of parameters in the final model. The slope and R^2 (1 – SEE/SST) for the relationship between predicted and observed tree growth, tree mortality and sapling abundance are also given.

functional composition and stand structure variables, although mean d.b.h. in broad-leaved deciduous forests and stand density in Mediterranean needle-leaved evergreen forests were not supported in the most parsimonious model (ΔAIC in Table 2). All of the models produced unbiased estimates of sapling abundance, and explained variance ranged from 9% for Mediterranean needle-leaved evergreen forests to 25% for other needle-leaved evergreen forests (Table 2).

The abundance of saplings was strongly influenced by FD and FI, with a comparable importance to temperature anomaly and stand structure (see the strength of evidence from ΔAIC in Table 2). Sapling abundance increased with FD, particularly in evergreen forests (Fig. 2b). Maximum sapling abundance occurred at low values of FI_{LMA} (i.e. stands dominated by broad-leaved species), except in needle-leaved evergreen forests broadly distributed in Europe (Fig. 2e). FD generally did not cause modification of the responses of sapling abundance to environmental conditions (see Table 2). In other needle-leaved evergreen forests broadly distributed across Europe, however, high tree diversity reduced responses of sapling abundance to potential evapotranspiration and temperature anomaly (Fig. 3a, b).

DISCUSSION

Demographic responses to functional diversity

Our results suggest that FD could directly influence tree growth and sapling abundance, while an influence of FD on mortality responses was not supported. The enhanced tree growth observed with FD is congruent with previous studies that found a positive effect of species richness on wood production across European forests (Vilà *et al.*, 2013), particularly those suggesting a large effect of diversity in Mediterranean forests (Ratcliffe *et al.*, 2016; Ruiz-Benito *et al.*, 2014a). The influence of diversity on demography could be due to complementarity mechanisms, which can be particularly strong in water-limited Mediterranean forests. As a proxy for potential complementarity effects, we used FD based on wood density, maximum tree height and seed mass. These traits have been identified as key for plant performance and indicators of life-history strategies (Hooper *et al.*, 2005; Swenson *et al.*, 2012). Increases in FD could be due to increases in the presence of individuals with contrasting functional traits (e.g. pine–oak mixed forests), which are particularly frequent in the Mediterranean and suggest niche

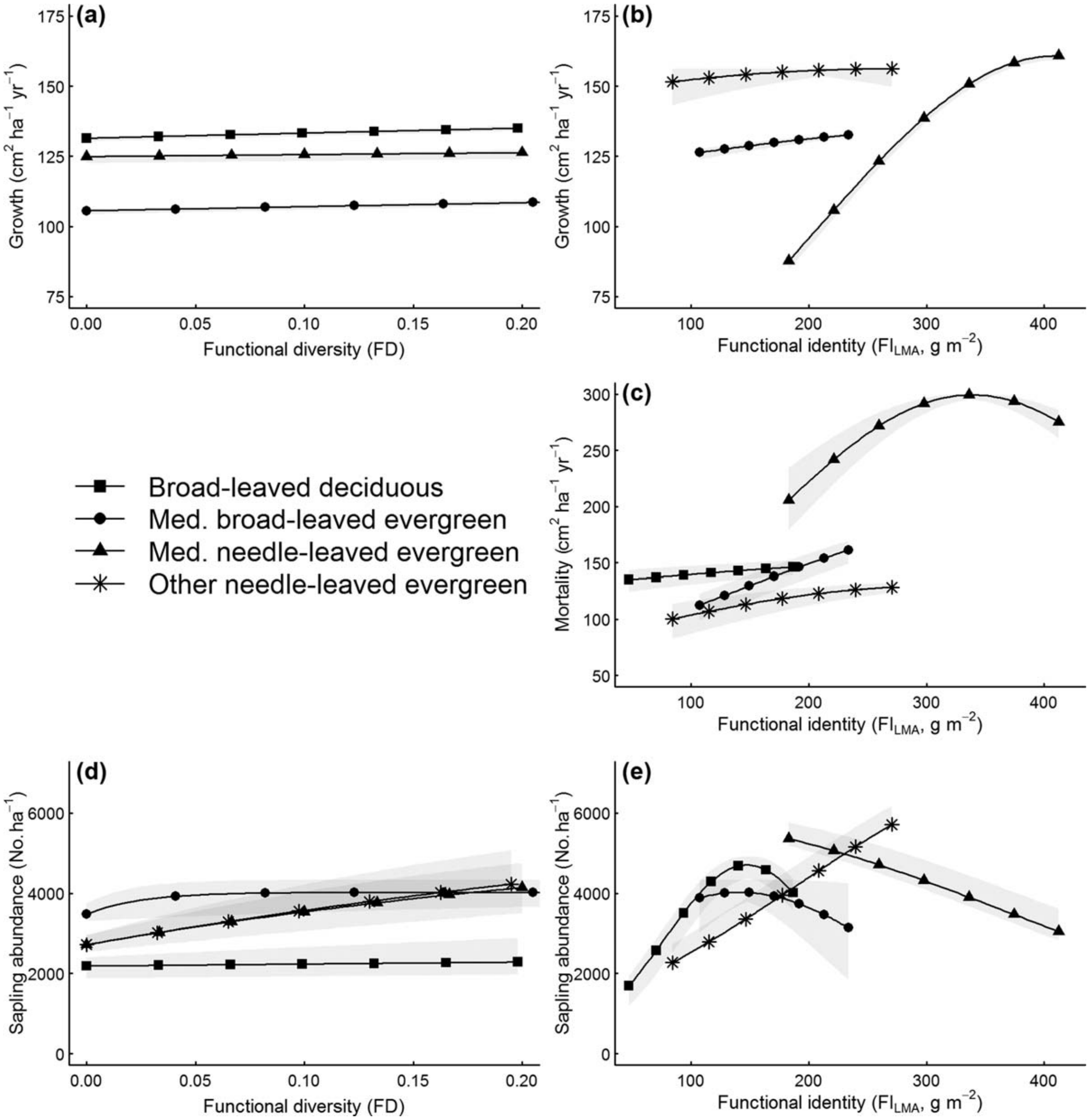

Figure 2 Predicted potential tree growth (cm^2 ha^{-1} year^{-1}), tree mortality (cm^2 ha^{-1} year^{-1}), and sapling abundance (no. ha^{-1}) by functional diversity (adimensional; a and b for growth and sapling abundance, respectively); and functional identity based on leaf mass per area (g m^2) for each forest type (c, d and e, respectively). The forest types include broad-leaved deciduous, Mediterranean broad-leaved evergreen, Mediterranean needle-leaved evergreen, and other needle-leaved evergreen forests. 95% confidence intervals are represented in grey. The predicted potential responses were computed between the minimum and maximum value of the explanatory variable of interest observed in each forest type (see parameter values in Table S5) and the scalars containing the rest of explanatory variables fixed at 1 (see equation 1).

partitioning as a plausible explanation for the positive effect of diversity in Mediterranean water-limited forests (Poorter *et al.*, 2012; Carnicer *et al.*, 2013).

Our results support the existence of a positive relationship between FD and sapling abundance in all the forest types studied (Table 2), suggesting that complementarity mechanisms may be driven by niche partitioning and facilitation processes. In addition, congruent with other studies (see Liang *et al.* 2007), we found tree diversity to have a greater influence on sapling abundance than on tree growth or mortality (Fig. 2). Sapling abundance in broad-leaved deciduous forests was relatively unresponsive to FD, but greater sapling abundance was observed in conifer-dominated and Mediterranean broad-leaved forests (Fig. 2). The strong demographic responses observed in conifer forests suggest that an abundance of saplings is favoured when there is a coexistence of functionally diverse species, which ultimately depends on climate, management and land-use history (e.g. pine–oak dominance in the Mediterranean region; Zavala & Zea, 2004; Sheffer, 2012). The successional status was not available from all the inventories, but we controlled for stand structure (i.e. including density and size-related effects) and the forest-type

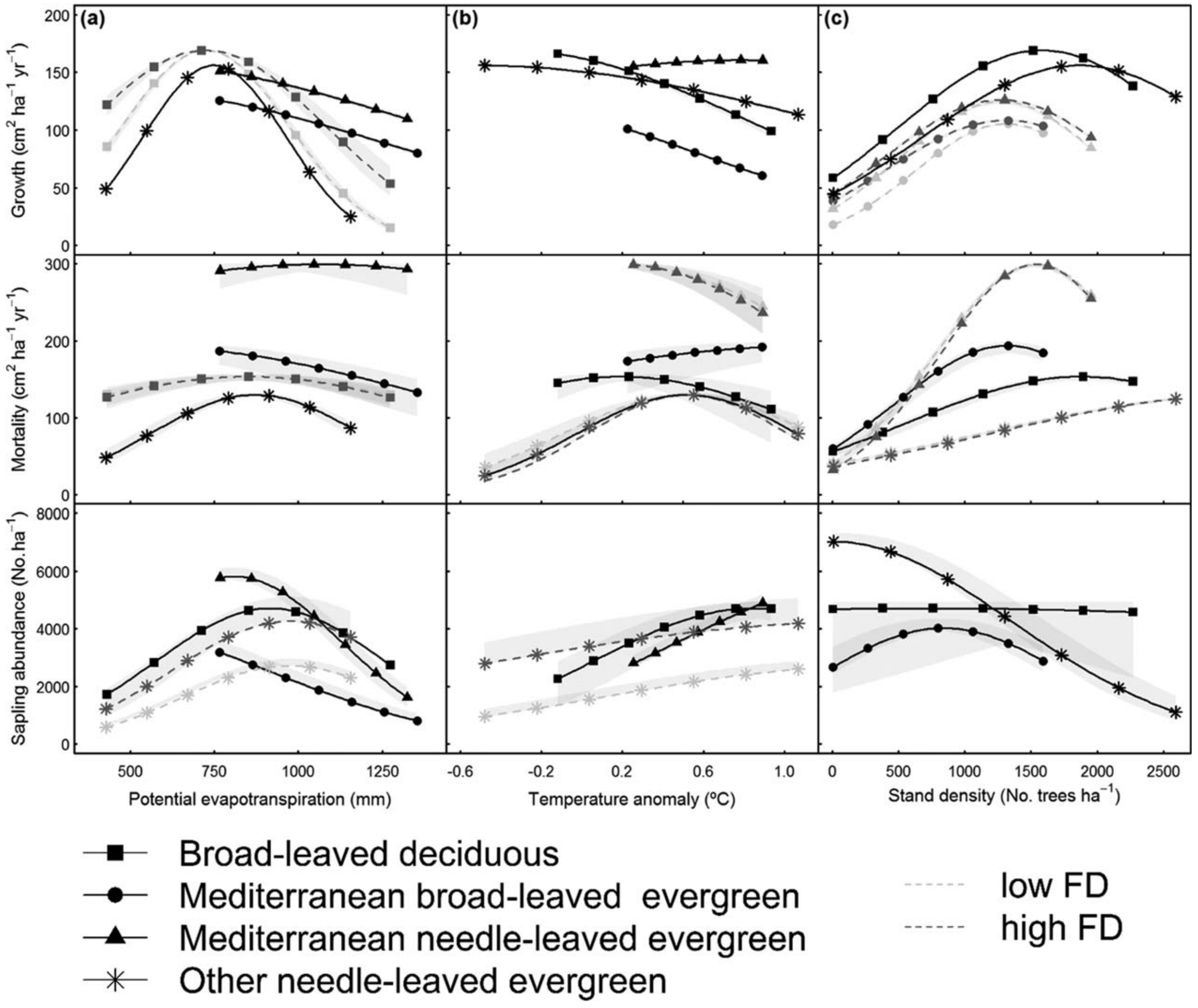

Figure 3 Predicted potential tree growth (cm^2 ha^{-1} year^{-1}), tree mortality (cm^2 ha^{-1} year^{-1}), and sapling abundance (no. ha^{-1}) by (a) potential evapotranspiration (mm), (b) temperature anomalies (°C), and (c) stand tree density (no. ha^{-1}) for each forest type at two combinations of functional diversity: monospecific forests (i.e. FD = 0) and diverse forests (i.e. FD = 0.2). Dashed lines indicate that the indirect effects of functional diversity determining demographic responses to environment were supported by the best model. Confidence intervals are shown in grey. The predicted potential responses were computed between the minimum and maximum value of the explanatory variable of interest observed in each forest type (see parameter values in Table S5) and the scalars containing the rest of explanatory variables fixed at 1 (see equation 1).

classification used is related to the general successional status of different species and their coexistence. Thus, further increments in FD may be due to changes in successional status with an increasing number of species and functional groups, which could lead to higher recruitment success promoting facilitation (Zavala *et al.*, 2011).

Demographic responses to functional identity

We observed the greatest mortality rates at high levels of leaf mass per area (i.e. stands dominated by needle-leaved species), but the highest abundance of saplings occurred at low values of leaf mass per area (i.e. stands dominated by broad-leaved species; see Fig. 2). These results suggest that stands with a large proportion of conifers experienced the highest mortality rates, as has already been observed at large spatial scales (e.g. Ruiz-Benito *et al.*, 2013). A possible explanation is that needle-leaved species generally have shorter life-spans than broad-leaved species and are less shade tolerant (Poorter *et al.*, 2012). Moreover, conifers have often been planted at high densities, which could underlie the low abundance of saplings and high mortality rates (e.g. Ruiz-Benito *et al.*, 2012, 2013). In addition, our results suggest that stands dominated by broad-leaved species experience greater abundances of saplings in all forest types studied (see Fig. 2 and Table 1; see also Vayreda *et al.*, 2013). An exception was found for conifers that are widely distributed in Europe, which showed a higher abundance of saplings in stands dominated by conifers rather than broad-leaved species. These are forests dominated by *Pinus sylvestris* and *Pinus nigra* which can constitute successional end-points under severe environmental conditions such as cold climates at high elevation or in shallow and rocky soils (e.g. Zavala & Zea, 2004).

Altogether, our results suggest that some Mediterranean needle-leaved forests may be experiencing the most important changes in species dominance because of high mortality in conifer-dominated stands and the high abundance of saplings observed in forests dominated by broad-leaved trees (Fig. 2). This may lead to increased dominance of oak species, which agrees with previous studies that found a severe limitation in recruitment for *Pinus* species, and an expansion in recruitment of *Quercus* species (Carnicer *et al.*, 2014). Furthermore, we found climate and functional identity to be more important for the abundance of saplings than stand structure in all forest types studied (Table 2). This finding may be due to the large climatic gradient covered and the influence of functional identity, which might reflect a successional trajectory along large climatic gradients (e.g. Ratcliffe *et al.*, 2016). These results are congruent with the observed increase in sapling abundance in broad-leaved forests and the increase in mortality rates in needle-leaved forests. However, further studies seeking the underlying drivers of multiple demographic processes and their effects on forest composition are needed to better understand the direction of and conditions for changes in vegetation.

Functional diversity underpins demographic responses to environmental conditions

Our models provide evidence of different demographic responses to tree density depending on the diversity of Mediterranean forests (see Table 2), with a smaller effect of extreme tree density on growth and mortality in more diverse forests (see Fig. 3). At high stand density increased mortality and decreased growth have been observed in European forests, probably due to high levels of competition for resources (Gómez-Aparicio *et al.*, 2011; Ruiz-Benito *et al.*, 2013). At low densities a combination of competition for limiting resources and greater exposure might boost interactions between climate and stand structure (e.g. Ruiz-Benito *et al.*, 2014b). Our result is consistent with previous studies that found that the positive effect of species richness on productivity was mediated by stand basal area (see Vilà *et al.*, 2013) and water availability (Pretzsch *et al.*, 2016). The trend observed suggests that diverse stands are able to pack more densely without showing strong declines in growth or increased mortality, which could be due to greater crown plasticity in mixed-species forests (see also Jucker *et al.*, 2015). Furthermore, our finding agrees with studies that found that water-use efficiency was a strongly promoted by diversity in drought-prone environments (Grossiord *et al.*, 2014b; Jucker *et al.*, 2016); this mechanism would be particularly important at high densities in Mediterranean forests.

We also found support for an effect of FD in ameliorating the negative effect of climate (i.e. potential evapotranspiration) and recent warming (i.e. temperature anomalies) on tree mortality and sapling abundance in some forests (see Table 2). These forests are widely distributed across Europe (i.e. broad-leaved deciduous and other needle-leaved evergreen forests) covering Mediterranean to boreal biomes (Fig. 1), and therefore experiencing a large gradient in potential evapotranspiration and temperature anomalies (see Fig. S2). We observed that tree diversity may modify demographic responses at the extremes of potential evapotranspiration, and recent climate warming was particularly important for coniferous forests dominated by *P. sylvestris* and *P. nigra*. It has been predicted that climate change will have a large impact on the demography and distribution of these species, particularly in mesic climates and rear edge distributions (Benito-Garzón *et al.*, 2013; Carnicer *et al.*, 2014). Relatively low increments in biomass have been reported in Mediterranean and boreal forests due to the effect of both water availability and minimum temperatures (Ruiz-Benito *et al.*, 2014b). Thus, modification of demographic responses to extreme climates by diversity may be particularly important in those forests where large impacts of increased temperature and reduced water availability are expected (e.g. Frank *et al.*, 2015).

Potential implications of diversity loss and species dominance under changing climate

Taken together, our results support the diversity hypothesis, suggesting that complementarity mechanisms play a key role in forest dynamics in addition to the effects on productivity or biomass that were the focus of previous studies (see e.g. Morin *et al.*, 2011; Ruiz-Benito *et al.*, 2014a). The importance of tree diversity for the functioning of European forests could have been underestimated, as we show that it can affect multiple demographic processes, including demographic responses to environmental conditions across Europe. Across the whole of Europe we observed higher growth rates and greater sapling abundance in more functionally diverse forests. Furthermore, the indirect effects of FD on demographic responses to environmental variation supported in our results also highlight the crucial task of maintaining functionally diverse forests. Here, we used growth and mortality rates based on basal area dynamics instead of biomass since basal area is a reliable proxy for biomass (e.g. Slik *et al.*, 2010), although further studies based on biomass may provide additional indications of the effects of FD on plant performance through complementarity mechanisms.

The influence of FI on demographic processes confirms the importance of the mass ratio hypothesis (i.e. dominance of species and contrasting functional groups). The variation in mortality and sapling abundance responses along FI gradients in Mediterranean pine forests suggests that forest dynamics could lead to a higher dominance of broad-leaved species in these forests. Our results highlight the importance of further studies seeking to better understand the underlying drivers and mechanisms of regional changes in forest dominance, particularly the mechanisms of species coexistence and maintenance of diversity under a changing environment at large-spatial scales.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Further details regarding the National Forest Inventories used.
Appendix S2 Further methodological details.
Table S1 Main characteristics of the sampling design from the five National Forest Inventories used in this study.
Table S2 List of species present in the plots of the National Forest Inventories included in the analyses.
Table S3 List of initial set of 27 climatic predictors.
Table S4 Trait data used in the study.
Table S5 Estimated parameters and 2-unit support intervals (in brackets) for the best tree growth, tree mortality models and recruitment models.
Fig. S1 Spatial distribution of the response variables in the National Forest Inventories.
Fig. S2 Spatial distribution of the predictor variables in the National Forest Inventories.
Fig. S3 Box-whisker plots of tree growth, tree mortality and sapling abundance along explanatory variables.
Fig. S4 Mean value of the functional traits depending on leaf characteristics used to define forest types.
Fig. S5 Histograms of tree growth, tree mortality and sapling abundance.

BIOSKETCH

Paloma Ruiz-Benito is a PLANT Fellow (http://www.plant-fellows.ch/) in the Biological and Environmental Sciences Division at the University of Stirling, UK. She is currently studying drought-induced effects on species demography and distribution in European forests, in collaboration with The Leverhulme International Network project on extreme drought impacts on forest dieback (http://www.biogeo.org/ASJ/Dieback.html) and the European FUNDIV project (http://www.fundiveurope.eu/).

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APPENDIX 1: REFERENCES FOR THE CLIMATE AND TRAIT DATA USED IN THIS STUDY

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