Climate change could negate positive tree diversity effects on forest productivity: A study across five climate types in Spain and Canada

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ABSTRACT

A positive relationship between tree diversity and forest productivity is reported for many forested biomes of the world. However, whether tree diversity is able to increase the stability of forest growth to changes in climate is still an open question. We addressed this question using 36,378 permanent forest plots from National Forest Inventories of Spain and Québec (Eastern Canada), covering five of the most important climate types where forests grow on Earth and a large temperature and precipitation gradient. The plots were used to compute forest productivity (aboveground woody biomass increment) and functional diversity (based on the functional traits of species). Divergence from normal levels of precipitation (dryer or wetter than 30-yr means) and temperature (warmer or colder), were computed for each plot from monthly temperature and precipitation means. Other expected drivers of forest growth were also included. Our results show a significant impact of climate divergences on forest productivity, but not always in the expected direction. Furthermore, although functional trait diversity had a general positive impact on forest productivity under normal conditions, this effect was not maintained in stands having suffered from temperature divergence (i.e. warmer conditions). Contrary to our expectations, we found that tree diversity did not result in more stable forest's growth conditions during changes in climate. These results could have important implications for the future dynamics and management of mixed forests worldwide under climate change.

INTRODUCTION

Forests are among those ecosystems predicted to suffer the most from added stress impacts following global change, such as drought, insect and disease outbreaks, and invasive species, among others (Choat et al., 2012). Increases in the frequency, duration, or severity of drought or extreme temperature could alter the composition, structure, and distribution of forests in many regions, as well as their functioning and ultimately the production of services upon which humanity depends (Allen et al., 2010; Thom and Seidl, 2016). In fact, some of those anticipated changes are already observed in some forest ecosystems, such as increased mortality following climate-change induced drought (Peng et al., 2011; Vayreda et al., 2012; Grimm et al., 2013).

There is considerable interest in evaluating the role of biodiversity in promoting ecosystem functions and services, and the biodiversity - ecosystem functioning (BEF) relationship has seen considerable interest, and controversy, for over two decades (Symstad et al., 2003; Reiss et al., 2009). The hypothesis that increased producer diversity leads to increased producer productivity is now accepted with high confidence for a variety of systems, although limitations and key research needs identified early are in several cases still relevant today (Hooper et al., 2005; Balvanera et al., 2014). Forests did not escape the trend, and have been under the lens of some recent large-scale observational research, testing the hypothesis that more diverse forests are more productive (Paquette and Messier, 2011; Vilà et al., 2013; Liang et al., 2016) and produce more ecosystem services (Gamfeldt et al., 2013; Ruiz-Benito et al., 2014). The hypothesized effect of biodiversity on growth is linked to facilitation and competition reduction, together forming complementarity (including niche partitioning and positive feedbacks on resource supply). Diversity effects on growth would also be dependent on the identity of the species present (sampling, or selection effect) due to dominant species driving ecosystem functioning (Roscher et al., 2012). These two mechanisms have been demonstrated in many ecosystems, with complementarity often being the most important (Reich et al., 2001; Cardinale et al., 2011). However, these positive effects are not always found, and may depend on site properties such as water and nutrient availability (Forrester et al., 2013; Pretzsch et al., 2015).

Most studies addressing the potential effects of tree diversity on forest productivity have been tested under stable conditions. They show a generally positive effect of biodiversity on forest productivity, but which can vary in size and even sign among biomes or regions, at the regional level (Paquette and Messier, 2011; Vilà et al., 2013) and across the world (Liang et al., 2016). However little has been achieved regarding the potential role of biodiversity in reducing the vulnerability (or in increasing stability) of forests to changes in climate (e.g. drought events), an issue raised early in BEF literature (Hooper et al., 2005). Vulnerability to stress has been linked to the portfolio effect (insurance hypothesis), where more diverse ecosystems are thought to better cope with stress because diversification minimizes the risk of a given function (e.g. growth) to be drastically affected (Thibaut and Connolly, 2012; Isbell et al., 2015). An increased capacity to cope with stress could also be achieved through complementarity or facilitation using the same mechanisms described above in stable conditions (Loreau and de Mazancourt, 2013). For example a greater water-use efficiency was observed for mixtures growing in dry conditions, which could lead to the same communities being better able to face a further decrease in water availability by further increasing their efficiency (Grossiord et al., 2014b). But those mechanisms could be altered, or even reversed, if the stable conditions that favoured them and the associated assemblage of species are changed, for example following climate change.

Another important consideration in BEF literature is the importance of species identity as well as their functional traits (Hooper et al., 2005). Diversity effects are intimately linked to the functional traits of species, at the core of a mechanistic understanding of biodiversity effects (Reiss et al., 2009; Loreau and de Mazancourt, 2013), because they link species to the role they play in the ecosystem and influence processes at higher organizational levels (Díaz et al., 2004; Violle et al., 2007). Evidence is accumulating that functional trait derived metrics of diversity, such as functional trait diversity (FD) and functional identity (measured using community weighted means - CWM) are needed to better assess diversity effects (Mokany et al., 2008; Tobner et al., 2014; Paquette et al., 2015).

This study aimed to analyse: (*i*) how functional trait diversity, climate and recent divergence in climate with respect to normals affect forest productivity and (*ii*) whether more diverse forests are more stable (i.e. capable of maintaining productivity) when facing stress due to either or both decreased precipitation levels and warmer conditions. We did so using data from 36,378 permanent survey plots in forests of Spain and Québec (Eastern Canada). Both datasets are of high quality, cover a large bioclimatic gradient and include repeated measures of the same trees over time, making them particularly suitable for testing these questions.

METHODS

Forest survey datasets and estimation of net productivity

The study was conducted in the forested areas of Québec (Eastern Canada) and peninsular Spain (i.e., excluding the Canary and Balearic Islands). These include five major climate types based on the Köppen-Geiger climate classification system (Kottek et al., 2006): (1) steppic (*Bsk* type), (2) dry Mediterranean (*Csa* and *Cfa* types), (3) humid Mediterranean (*Cfb* and *Csb* types) for Spain, (4) temperate (*Dfb* type) and (5) boreal (*Dfc* type) for Québec (Fig. 1).

Forest data from Québec and Spain were obtained from large forest inventory datasets. The Québec forest inventory was initiated in the 1970's and covers all public lands (up to the northern limit for timber allocations; Fig. 1A) including over 36,000 plots measured approximately every ten years (Duchesne and Ouimet, 2008). During surveys, all trees with a diameter at breast height (DBH) above 9.1 cm are numbered, species identified, and their DBH measured within 400 m^2 circular plots. To match with data from Spain, only data from the last two sets of measurements that correspond to the third (ca. 1990-2000) and fourth (ca. 2000-2010) inventories were used.

In Spain, data were obtained from the Spanish second and third National Forest Inventory (NFI; 1986-1996 and 1997-2007, respectively). The NFI consists in a network of plots (> 50,000) distributed across the forested area of Spain on a 1-km^2 grid (Ministerio de Medio Ambiente, 2007). The sampling method uses circular plots of which radius varies according to the DBH of the target tree: all trees with DBH ≥ 7.5 cm are measured within 5 m of the plot center, additional trees with DBH ≥ 12.5 cm are measured in a circular band 5 to 10 m from the center, whereas trees with DBH ≥ 22.5 cm and with DBH ≥ 42.5 are also considered within 10-15 and 15-25 m bands, respectively. As in Québec, the Spanish NFI plots are measured at an interval of approximately ten years.

We selected pairs of plots without sign of significant disturbance (such as fire) and that had not been subjected to human interventions between the two surveys. We also excluded from the analysis plots dominated by exotic species and sparse stands with basal area $G < 2$ m^2 ha^{-1}. After selection, the total number of plots measured twice used in this study was 7,127 and 29,251 for Québec and Spain, respectively (Table 1).

For each individual pair of plots, three variables were calculated to estimate changes in aboveground woody biomass (excluding leaves) through time, i.e. net productivity: (1) *Aboveground increment due to tree growth* (Mg ha^{-1} y^{-1}) that is the sum of the aboveground woody biomass increment of the surviving trees between the two measurement periods (t_1 and t_2) and ingrowth (i.e. recruit trees reaching the minimum DBH threshold), (2) *Aboveground biomass loss due to tree mortality*, that included those trees that were alive at t_1 but were dead or had disappeared (rare; assumed to be dead) at t_2, and (3) *Net aboveground woody biomass productivity* (Mg ha^{-1} y^{-1}) calculated as the difference between the two former variables. This last quantity forms our response variable for net productivity.

The total biomass of the trunk, bark and branches of each individual tree present in the plot was computed from DBH using species-specific allometry equations developed by Lambert et al. (2005) for Québec and by Gracia et al. (2004) and Montero et al. (2005) for Spain. For some uncommon species without published equations we used parameters and generalized equations obtained for the functional groups to which they belong (i.e. conifers, deciduous or sclerophyllous species) (see Paquette and Messier (2011) and Vayreda et al. (2012) for further details). In addition to biomass increment, we also calculated plot basal area (G, m^2 ha^{-1}) to account for density.

Functional trait diversity indices

Data on functional traits were collected from published sources for the tree species present in both regions: wood density (Wd, g cm^{-3}), seed mass (Sm, mg - natural-log transformed), maximum tree height (H_{max}, m), and leaf mass area (LMA, g m^{-2}). These traits have been shown to be related to forest productivity, including the forests studied here (Paquette and Messier, 2011; Ruiz-Benito et al., 2014; Paquette et al., 2015). Wood density and seed mass are closely related to life history strategies (Swenson and Enquist, 2007; Chave et al., 2009; Ben-Hur et al., 2012). The same is true with maximum height which also relates to vertical stratification and the use of light (Sapijanskas et al., 2014; Kunstler et al., 2016), while leaf mass per area is related to resource acquisition (Shipley et al., 2006). Together these traits form a "plant economics spectrum" defined by trade-offs between fast and slow growing strategies (Reich, 2014) with globally consistent effects on competition among forest trees (Kunstler et al., 2016). We computed functional trait diversity using the functional dispersion index (Laliberté and Legendre, 2010) based on trait dissimilarity among species in the first three traits (*Wd, Sm* and H_{max}) as often used in the BEF literature since variation in their related strategies is posited to increase niche partitioning and complementarity. Functional identity was computed using community weighted means of trait values (CWM; Lavorel et al., 2008) for H_{max} and *LMA* to test the hypothesis that mean trait values drive community tolerance to drought (e.g., small trees or thick leaves that increase water-use efficiency and decrease the risks associated with water-stress). Each has been linked to different components of biodiversity effects. Complementarity effects that promote species coexistence and competition reduction are best explained by the functional trait diversity index, whereas selection effects relate to the mass ratio hypothesis, whereby ecosystem functions are driven by the traits of dominant species, and are best assessed with the functional identity of the community (*CWM*) (Roscher et al., 2012; Tobner et al., 2016).

Divergence from 30-year climate normals and environmental variables

Climatic data for this study were obtained from Willmott and Matsuura (2001) which provides monthly temperature and precipitation means for every year for the last decades at a spatial resolution of 0.5 x 0.5 degree of latitude/longitude. We assigned mean temperature and precipitation values for each plot based on their geographical coordinates. The same source was used to assess temperature and precipitation trends between study periods. We determined for each plot the absolute temperature trend (ºC) which was calculated as the difference between the mean temperature for the study period and the mean temperature for a reference period of 30 years before the first sampling period. We also calculated a relative precipitation trend (%) as the ratio of the difference in precipitations between the study period and the reference period divided by the reference period. These trends were assessed only for the summer season (mean temperature trend of June, July and August). In addition to climatic characterization, we collected for each plot the slope (º) and the depth of the organic layer (cm). Both variables were considered representative of environmental site conditions and were equally measured in Québec and Spanish surveys.

Analyses

The response variable we used to test our main hypothesis was net annual aboveground productivity based on 10-year intervals. Explanatory variables were the divergence from normal levels of precipitation (dryer or wetter than 30-yr means) and temperature (warmer or colder than the past 30 years), functional trait diversity, and their interactions.

Appropriate confounding factors such as mean annual temperature and total precipitation, local growing conditions (slope, depth of the organic layer), and stand basal area (*G*), were also included in our analysis.

For each climate type, we used general linear models (GLM) to analyze the relationship between net annual aboveground productivity, the different explanatory variables, and the interactions considered (those between climatic divergences and diversity variables) (see Table 1 for the list and mean values of all variables initially considered). A stepwise model selection was applied starting with a saturated model and removing least significant variables until no further decrease in the Bayesian Information Criterion (BIC) was observed. We considered the fit of models to be equivalent within 2 BIC units. All statistical analyses were made within the R environment (R Core Team, 2015).

We then checked for multicollinearity in the final model using variance inflation factors (VIFs) without interaction terms; all VIFs obtained were lower than 3, i.e. a low correlation (Heiberger and Holland, 2015). Furthermore for each final model, latitude and longitude were used to model the correlation structure of the errors (Venables and Ripley, 2013) using generalized least squares (function gls in package nlme) and a linear spatial correlation structure. Only in one case (boreal forests) was the model improved (increase in AIC ≥ 84 units) but the coefficients for all other factors were not different from the original GLM model and so only that model is shown for simplicity. R^2 and VIFs of the selected model were obtained using the general linear model (function lm in R).

RESULTS

Global trends among the five climate types.

There was a clear geographic pattern for the distribution of net productivity according to climate. In peninsular Spain, net productivity was mainly driven by precipitation and temperature, showing an increase in productivity from the south-east (dryer and warmer) to the north-northwest (wetter and colder), while in Eastern Canada net productivity was driven by temperature, decreasing from south to north (Table 1). In peninsular Spain the lowest net productivity values occurred in the steppe (semi-arid) climate, characterized by high temperatures and very low precipitation (~ 360 mm). In the dry Mediterranean climate precipitation was twice that of the steppes and temperature was similar, leading to a significant increase in net productivity. Finally, in the Humid Mediterranean climate temperature was clearly lower (by more than 4 ºC) and precipitation was higher (by almost 200 mm per year), which allowed the highest net productivity of the five areas analyzed. In Eastern Canada, the geographical productivity pattern also followed a south-north gradient, but opposite to the Spanish, where net productivity decreased slightly with decreasing temperature. As expected, the largest basal areas were found in the most productive climates. There was a clear increasing gradient of organic layer depth with increasing precipitation and decreasing mean annual temperature, going from 1.4 cm deep in the steppe of Spain to 20.5 cm in the boreal forest of Québec.

Temperature and precipitation divergences were clearly stronger in Spain than in Québec, with a 1°C temperature increase in Spain compared to 0.3°C in Québec and a decline in precipitation between 5 and 20% in Spain compared to only 2 to 3% in Québec. Finally, functional trait diversity was lowest in the steppe climate of Spain and highest in the temperate climate of Québec. Community weighted means for maximum height (CWM_{maxH}) were very similar among climates varying from a low of 21 m in the dry Mediterranean climate to a high of 25 m in the temperate climate. The CWM_{LMA} was lowest in the temperate climate, dominated by broadleaf angiosperms, and highest in the boreal, dominated by needle-like gymnosperms (Table 1).

Stand density, soil and climatic factors affecting net productivity

Variance explained by the models was always higher than 50%, ranging from 52% in the temperate to 72% of the humid Mediterranean climates (Table 2). The effect of basal area was always strong, with a positive effect on net productivity, especially in the Spanish climates (Table 2). Climatic variables (average temperature and annual precipitation) had a significant effect everywhere except in the steppes of southern Spain. In all other climate types, annual precipitation had a positive effect on net productivity. On the other hand, mean temperature had a positive effect on net productivity in the boreal, temperate and humid Mediterranean climates, while in the dry Mediterranean it was negative. In all climates, slope had a negative effect on net productivity, while the depth of the organic layer had a positive effect in the Mediterranean climates and a negative effect in the temperate and boreal climates.

Divergence from 30-year climate normals and diversity metrics affecting net productivity

The direct effect of recent changes in precipitation or temperatures with respect to the previous 30 years was not strong (Table 2). Thermal divergence showed a positive effect on net productivity in the dry Mediterranean and temperate climates, and negative in the humid Mediterranean. The effect of the precipitation divergence was significant and positive for the humid Mediterranean climate, and negative for the Boreal climate.

Functional trait diversity showed a positive effect on net productivity in all climates except in the steppes, where it was not significant (Table 2). The variables relating to functional identity, measured through community-level weighted means (*CWM*), showed different patterns in the five climates. CWM for maximum height had a positive effect in intermediate climates and no effect in the extreme climates of both regions. The effect of mean LMA on net productivity went from positive in Peninsular Spain (but no effect in the steppe climate) to negative in Québec, indicating that conifers with high LMA in Spain and broadleaves with low LMA in Eastern Canada were the most productive.

Effects of functional trait diversity in mitigating climatic divergence effects on net tree productivity

In order for diversity to show a mitigation effect on net tree aboveground productivity, our GLM model should indicate a significant functional diversity*divergence interaction. There was no significant effect for the interaction between functional trait diversity and the precipitation divergence (Table 2). However, some significant interactions were found between functional diversity and the temperature divergence for three climates. In all cases, net productivity in the more diverse plots was negatively affected by the divergence in temperature (Fig. 2). We recall that this divergence (increased temperature) had in two cases a mean positive impact on net productivity (i.e. it was not stressful), so what these significant interactions actually show is that more diverse forests were more productive on average, except where temperatures had increased through recent warming, whereas the same increase in temperature had a positive impact in less diverse plots. In the humid Mediterranean, the effect was similar except that diversity had no effect where temperature had increased, causing lower productivity throughout (Fig. 2).

DISCUSSION

The effect of climate on growth

Our study supports previous findings of positive effects of tree diversity on forest productivity (Vilà et al., 2007; Lei et al., 2009; Paquette and Messier, 2011; Gamfeldt et al., 2013; Vilà et al., 2013; Ruiz-Benito et al., 2014; Liang et al., 2016). As expected, the net productivity pattern was also conditioned by climate; from warmer to colder climates in Québec, and from hot and dry to cooler and more humid conditions in Spain. Where significant, increased temperature had a positive impact on net productivity, except in the humid Mediterranean (Table 2). This was expected for Québec forests where a longer season and increased temperatures, combined with sufficient water supplies, would improve growing conditions (Grimm et al., 2013). In contrast, the result obtained for dry Mediterranean areas is difficult to explain. Within this climate, forest productivity was found to be the lowest in the warmest areas (Table 2) but, contrary to expected, forests responded positively to temperature increases. This could be explained by the wide average period we used to compute divergence (~10 years) which could hide changes in growth associated to temperature variations occurring over shorter periods. Only in the humid Mediterranean did we find a significant negative effect of reduced precipitation as predicted, as well as from increased temperature. During the summer, these forests are normally able to cope with warm conditions because of a sufficient water supply. However, decreases in pluviometry and increased temperature lead to water stress, reduced growth and possibly increased mortality (Vayreda et al., 2012) (Table 2). The opposite effect was found in boreal forests, where recent increases in precipitations caused declines in productivity. These systems do not suffer from lack in precipitations; rather they grow in soils that are often waterlogged – due to poor drainage, limited evapotranspiration and a short growing season – so an increase in precipitation would worsen growing conditions and increase mortality where water may accumulate. We expected the reverse response for water-limited steppes and dry Mediterranean forests (i.e. the same as in the humid Mediterranean). However variations in precipitation levels did not affect net productivity in these climates, meaning either that the forests were already well equipped to face variations in precipitations (Vayreda et al., 2012), that precipitations did not vary much within those areas through time or, on the contrary, that normal variation in climate over the previous 30 years were on average larger than the divergence computed over 10 years.

Recent climatic divergences and the effects of functional trait diversity

Our working hypothesis was that more diverse forests can better cope (i.e., their net productivity would be less affected) with recently induced increasing levels of drought or higher temperatures, than less diverse forests. The interactions found between temperature divergences and diversity were on the opposite direction of our hypothesis. While in most cases an increase in temperature did not affect negatively tree net productivity, only the forests with the lowest diversity were either less affected, or actually able to maintain or even increase net productivity with increasing temperature (Fig. 2). In contrast, those forest stands with higher functional trait diversity responded in the opposite direction, showing in all cases pronounced reduction in growth with increasing temperature. This result suggests that the hypothesized positive effect of diversity on net productivity might not occur with increasing climatic divergences; i.e. the current benefit of growing together in a stable climate may not hold when conditions change (Grossiord et al., 2014b). Indeed, some recent studies suggest that when facing climatic divergences, species mixtures that were favouring complementarity effects may start competing for resources and negate the diversity effects found under the previous stable conditions (Jucker et al., 2014). This could be the result of the higher transpiration induced by mixed tree species compared to monoculture (Kunert et al., 2012). However, others have found the opposite (Lebourgeois et al., 2013), with some finding positive effects of diversity only during dry (vs wet) years (Grossiord et al., 2013; Grossiord et al., 2014a), or only in drought-prone environments (Grossiord et al., 2014b). Interestingly however, Grossiord et al. (2014a) reported a positive effect of diversity in dry years via an increase of the water use efficiency, which incidentally did not provide any buffering against the observed reduction in productivity (increments in basal area), as we also found. This suggests that resources are better accessed and exploited in mixtures which may then lead to detrimental biodiversity effects where soil water can be more intensively exhausted during droughts by the more efficient mixtures (Grossiord et al., 2014a). Our results reported only aboveground growth and it is possible that mixtures invested more belowground with increasing temperature divergence to better cope with the possible increasing evapotranspiration. This is supported by results from a controlled experiment where tree mixtures were found to allocate proportionally less belowground than monospecific stands under optimal growing conditions (Archambault, 2016).

In summary, our study found a general positive effect of tree diversity on stand productivity under stable conditions, and showed different responses of forests to temperature and precipitation divergences depending on the considered climatic zone. However, and contrary to our expectations, we found an overall negative effect of tree diversity on the capacity of the stands to maintain productivity when faced with climatic divergences. Further research is required to assess the underlying mechanisms behind these unexpected patterns.

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TABLE LEGENDS

Table 1. Species composition and values of the different variables in the five climate types analyzed.

Table 2. GLM model results for factors and interactions explaining net aboveground tree productivity in forests of the five climates studied. ***p<0.001; **p<0.01; n.s. not significant.

FIGURE LEGENDS

Figure 1. Distribution of sampled plots and climates (in different colors) covered in (b) Québec and (c) Spain. Note that in Québec, sampling covers the land up to the limit of the exploitable forest (ca. latitude 52°).

Figure 2. 3D changes in net aboveground productivity (production; Mg ha^{-1} yr^{-1}) in relation to functional trait diversity and temperature trends as found in some biomes.

Table 1. Species composition and values of the different variables in the five climate types analyzed.

	Steppe (semi-arid) (BSk)	**Dry Mediterranean (Csa + Cfa)**	**Humid Mediterranean (Cfb+ Csb)**	**Temperate (Dfb)**	**Boreal (Dfc)**
Most abundant tree species	*Pinus halepensis* *Quercus ilex*	*Quercus ilex* *Pinus halepensis* *Pinus pinaster* *Quercus suber*	*Pinus sylvestris* *Quercus ilex* *Pinus nigra* *Pinus pinaster*	*Acer saccharum* *Abies balsamea* *Acer rubrum* *Betula alleghaniensis*	*Picea mariana* *Abies balsamea* *Betula papyrifera* *Populus tremuloides*
Net productivity (Mg ha^{-1} yr^{-1})	0.87 ± 0.75	1.43 ± 1.59	2.86 ± 2.62	1.97 ± 0.14	1.77 ± 0.13
Basal area (*G;* m² ha^{-1})	8.0 ± 5.7	10.9 ± 8.8	18.5 ± 12.8	22.8 ± 8.7	18.2 ± 9.4
Annual precipitation (mm)	361 ± 48	668 ± 174	827 ± 300	1015 ± 109	993 ± 166
Mean annual temperature (ºC)	14.3 ± 1.4	14.5 ± 1.6	10.4 ± 1.6	2.7 ±1.3	-0.8 ± 1.5
Slope (º)	18.8 ± 9.7	16.0 ± 10.2	18.9 ± 11.2	12.7 ± 11.0	12.2 ±11.4
Organic layer depth (cm)	1.35 ± 1.10	1.78 ± 1.55	2.86 ± 2.26	12.1 ± 18.1	20.5 ± 20.7
Temperature trend (ºC)	0.83 ± 0.28	1.11 ± 0.41	1.11 ± 0.42	0.31 ± 0.31	0.31 ± 0.27
Precipitation trend (%)	-9.2 ± 13.2	-20.5 ± 16.8	-4.5 ± 7.3	-1.7 ± 7.7	-3.3 ± 6.0
Species richness	1.13 ± 0.4	1.52 ± 0.83	1.88 ± 1.09	4.91 ± 2.03	2.52 ± 1.27
Functional trait diversity	0.11 ± 0.35	0.36 ± 0.56	0.57 ± 0.63	0.90 ± 0.33	0.46 ± 0.28
CWM_{maxH}	23.2 ± 1.42	20.9 ± 3.01	23.2 ± 4.43	25.1 ± 3.87	21.5 ± 1.84
CWM_{LMA}	227.9 ± 27.4	206.7 ± 76.7	190.9 ± 86.3	136.0 ± 67.9	240.25 ± 60.9
N plots	1,603	12,585	15,063	4,486	2,641

Table 2. GLM model results for factors and interactions explaining net aboveground tree productivity in forests of the five climates studied. ***p<0.001; **p<0.01; n.s. not significant.

	Steppe (semi-arid) (BSk)		**Dry Mediterranean (Csa + Cfa)**		**Humid Mediterranean (Cfb+ Csb)**		**Temperate (Dfb)**		**Boreal (Dfc)**	
	t-value	**Sign.**	**t-value**	**Sign.**	**t-value**	**Sign.**	**t-value**	**Sign.**	**t-value**	**Sign.**
(Intercept)	-47.7	***	-32.8	***	-47.5	***	33.3	***	59.9	***
Basal area	46.3	***	101.0	***	145.6	***	46.6	***	38.5	***
Annual Precipitation			4.3	***	13.3	***	5.2	***	5.8	***
Mean annual Temperature			-8.6	***	12.3	***	10.7	***	17.3	***
Slope	-4.5	***	-3.0	**	-11.6	***	-4.8	***	-2.8	**
Organic layer depth	2.6	**	12.1	***	10.0	***	-8.8	***	-5.8	***
Temperature trend (TT)			7.7	***	-4.0	**	4.0	***	0.7	n.s.
Precipitation trend (PT)					7.1	***			-8.8	***
Functional diversity (FDis)			12.8	***	10.42	***	3.8	***	4.6	***
$\mathbf{CWM_{maxH}}$			21.2	***	22.1	***	7.5	***		
$\mathbf{CWM_{LMA}}$			6.8	***	3.7	***	-12.3	***	-16.7	***
TT x FDis					-6.2	***	-4.7	***	-3.4	***
PT x FDis										
d.f.	1,599		12,502		15,017		4,381		2,587	
$\mathbf{R^2}$	0.60		0.64		0.71		0.52		0.69	
BIC	2,590		23,422		24,953		-13,669		-9,291	

Note: Only significant effects are shown except where involved in a significant interaction (one instance).

Figure 1. Distribution of sampled plots and climates (in different colors) covered in (b) Québec and (c) Spain. Note that in Québec, sampling covers the land up to the limit of the exploitable forest (ca. latitude 52°).

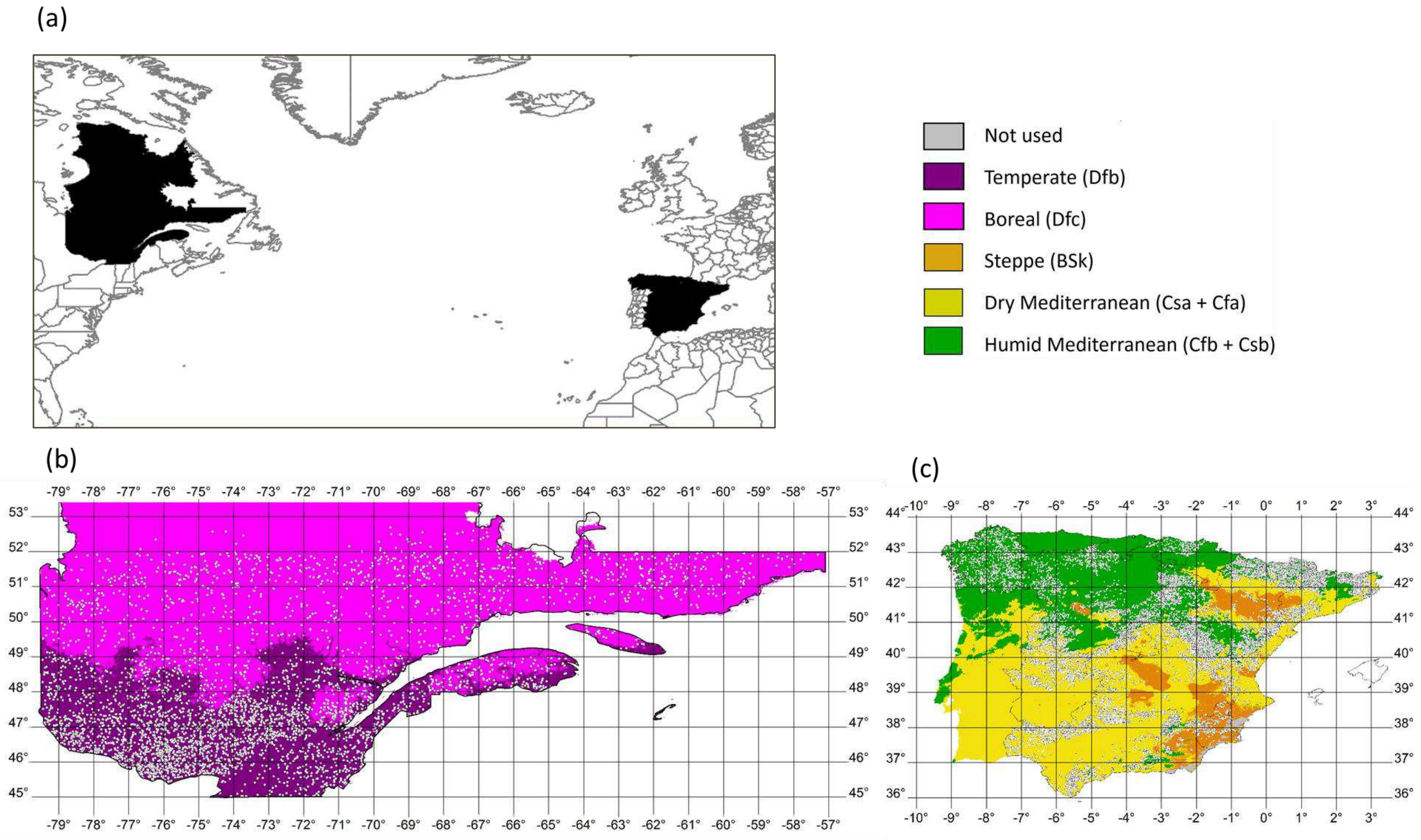

Figure 2. 3D changes in net aboveground productivity (production; Mg ha^{-1} yr^{-1}) in relation to functional trait diversity and temperature trends as found in some biomes.