Relationship between projected changes in future climatic suitability and demographic and functional traits of forest tree species in Spain

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Abstract The response of plant species to future climate conditions is probably dependent on their ecological characteristics, including climatic niche, demographic rates and functional traits. Using forest inventory data from 27 dominant woody species in Spanish forests, we explore the relationships between species characteristics and projected changes in their average climatic suitability (occurrence of suitable climatic conditions for a species in a given territory) obtained by empirical niche-based models, under a business-as-usual climate change scenario (A1, HadCM3, 2001–2100). We hypothesize that most species will suffer a decline in climatic suitability, with a less severe for species (i) currently living in more arid climates or exhibiting a broader current climatic niche; (ii) with higher current growth rates; (iii) with functional traits related to resistance to water deficits. The analysis confirm our hypothesis since apart from a few Mediterranean species, most species decrease their climatic suitability in the region under future climate, characterized by increased aridity. Also, species living in warmer locations or under a wider range of climatic conditions tend to experience less decrease in climatic suitability. As hypothesized, a positive relationship was detected between current relative growth rates and increase in future climatic suitability. Nevertheless, current tree mortality did not correlate with changes in future climatic suitability. In contrast with our hypothesis, functional traits did not show a clear relationship with changes in climate suitability; instead species often presented idiosyncratic responses that, in some cases, could reflect past management. These results suggest that the extrapolation of species performance to future climatic

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scenarios based on current patterns of dominance is constrained by factors other than species autoecology, particularly human activity.

1 Introduction

Forecasting the ecological features of vegetation under future climate conditions is a major concern in the assessment of the impacts of global change (Bonan 2008). Any assessment may benefit from analyzing the relationship between the species ecological characteristics and the projected change in the occurrence in a given territory of suitable climatic conditions for such species (climatic suitability, hereafter). Projections of future species distributions may be obtained from empirical niche-based models. These models geographically extrapolate the current relationship between species distribution and environmental (mainly climatic) variables to expected suitable climatic conditions in the future via statistical modelling (Franklin 2010). These models may also be useful for analyzing how expected future conditions and current demographic trends correlate, thereby providing insights into the vulnerability of species to the new scenarios. In spite of its usefulness, the correspondence between plant traits and climate change response has scarcely been studied at present (f.i., Esther et al. 2010).

Empirical niche-based models have some methodological shortcomings, however. These statistical models do not directly consider the ecological processes that determine species distribution, they merely represent an estimate of future climatic suitability, based on the current relationship between species distribution and climate. Many factors, including dispersal constraints, biotic interactions, disturbance regime and human intervention, make significant contributions to species distribution but are not usually considered (Meier et al. 2010; Svenning et al. 2010). In addition, the assumption of climate-distribution equilibrium has been challenged by paleoecological studies suggesting shifts of species realized niche under natural climate change (Mellick et al. 2012). Finally, the variety and reliability of modelling procedures and the quality of data imply technical challenges (Elith and Graham 2009; Foody 2011).

Functional traits, including life-history traits, can help to characterize the ecological response of vegetation to climate change (Keith et al. 2008; Esther et al. 2010) although historical stochasticity, microsite conditions and demographic processes may mask this relationship, as can be seen in animals (Angert et al. 2011). Plant functional types have been extensively applied in the development of vegetation dynamics models at different scales (f.i., Prentice et al. 1992), often using a broad description of them, without any specific link to the species level. However, functional traits reflect specific environmental conditions—due, for example, to phenotypic plasticity or adaptation. Therefore, the analysis of the relationship between traits and environmental changes is expected to be context-dependent and should gain from trait estimations obtained from the target populations.

The fate of a given species is also likely to be influenced by the performance of its current populations. Population decline (i.e. high mortality rates or low individual growth) is an indicator of species vulnerability, particularly if the new climatic conditions are expected to increase abiotic stress (Allen et al. 2010). This could be the case with populations currently established at the southern edge of their distribution in the temperate regions of the Northern Hemisphere, where climatic projections forecast an overall increase in aridity (IPCC 2007). Alternatively, current low mortality and/or high growth rates could indicate that populations are robust enough to cope with the upcoming conditions—at least

in the short term -, or even that they are still responding positively to the new climatic environment (Doak and Morris 2010).

In this study we explore the relationship between projected changes in future climatic suitability due to climate change and demographic and plant functional traits of species. We estimate species climatic suitability from the climatic conditions modelled from species current pattern of distribution. We use 27 dominant woody species from forests in Spain, a Mediterranean region that is predicted to experience an overall increase in aridity in the coming decades (IPCC 2007; Giorgi et al. 2004; Felicisimo 2011). More specifically, we address whether the projected future changes in climatic suitability are related to:

(1) The current climatic conditions where dominant species are currently found. We hypothesize that due to an expected increase of aridity (i) climatic suitability will remain higher for species currently living in more arid climates, and (ii) the broader range of climatic conditions where species are currently found, the lower the projected loss of future climatic suitability.

(2) The current trends in demographic variables (plant growth and mortality). We aim to explore if future reduction in climatic suitability in a given territory could exacerbate current demographic trends leading to decline that are observed in populations of such territory. In the case of plant growth we hypothesize a positive relationship between growth rate and change in climatic suitability. We base this hypothesis on the fact that populations are already responding to climate trends that have the same direction as expected in the future (Jump et al. 2008, 2009).

(3) The functional traits of species (maximum tree height, wood density, specific leaf area, nitrogen content of leaves, leaf area and seed mass). We hypothesize that traits related to resistance to stress, particularly water deficit, will perform better in the future scenario of increasing aridity, that is, they would correlate accordingly with changes of climatic suitability.

2 Methods

2.1 Study area

The study area is continental Spain. The general climate is temperate, but there is a large elevation gradient, and the climate shows a wide variation from semiarid in the Southeast to humid and moderately cold in the Northwest, with different types of Mediterranean climate in the remaining area, where mountain ranges are common. There is also a continentality gradient, with hot summers and cold winters inland. Average annual temperature ranges between less than 5 °C on mountain peaks (up to ~3,500 m)—mostly in N Spain—to ca. 19 °C in the South. Total annual rainfall ranges between ca. 2,000 mm in the Northwest to less than 250 mm in the Southeast. The vegetation consists mostly of managed sclerophyllous, evergreen shrublands and broadleaf, deciduous, and coniferous forests.

2.2 Demographic, functional and climatic characterization of species

The final set of 27 species considered in this study (Supplementary material, Annex 1) was the result of a compromise between the information available from estimates of climatic

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suitability and the information on demographic traits provided by forest inventories. We only considered species for which at least 100 individual trees were re-measured in two successive inventories. Thus we focus on dominant species in these forests.

We used average tree growth and mortality as indicators of the species' current demographic trend in the territory, as described elsewhere (Martínez-Vilalta et al. 2010). Briefly, these parameters were obtained by comparing the second and third Spanish National Forest Inventories (IFN2, period 1986–96, and IFN3, period 1997–2007, respectively; Dirección General de Conservación de la Naturaleza 2006), which sampled the whole forested area of Spain (ca. $10.7 \cdot 10^6$ ha) at a density of approximately 1 plot km^{-2} following a regular design, (N=54,300). We excluded from the study those plots with evidence of forest management, i.e. cutting or thinning, in the plot or the surrounding area as recorded during the IFN3 survey (remaining N=40,373 plots). Plantation non-native species that are primarily grown for timber production in Spain were excluded from the analyses. Tree growth and mortality was only calculated from the adult individuals, with DBH >12.5 cm for species with typical tall trees (typical DBH >15 cm and typical height >10 m), and with DBH >7.5 cm for species with typical short trees or shrubs (typical DBH <15 cm and typical height <10 m) (Supplementary Material, Annex 1).

Species growth was estimated as the average of the relative growth rate (RGR) of the trees belonging to each species. RGR was calculated for each individual tree as $(\ln[DBH_{IFN3}] - \ln[DBH_{IFN2}]) / \text{time}$, where DBH_{IFN2} and DBH_{IFN3} are the diameters at breast height measured in the second and third Spanish Forest Inventories, respectively, and time is the time interval between measurements.

Annual mortality rate (MR) was calculated as $(\ln[N_{IFN2}] - \ln[N_{IFN3}]) / \text{time}$, where N_{IFN2} is the number of trees of a given species that were recorded in the IFN2, N_{IFN3} the number of those that were still alive in the IFN3, and time is the interval between surveys. Although the precise period may vary among plots, we considered these estimations to reflect the demographical tendencies at a decadal scale during the whole surveyed period. The different sample size used for each species did not imply a significant bias in MR estimations (Martínez-Vilalta et al. 2010). Tree size distribution had no relevant overall effect on the estimated demographic rates (Martínez-Vilalta et al. 2010).

We used the following functional traits (cf. Westoby and Wright 2006): maximum tree height (hereafter, height, Hmax) (m), wood density (WD) (g·cm^{-3}), specific leaf area (SLA) (mm^2·mg^{-1}), nitrogen content of leaves (Nmass) (% mass), leaf area (LA) (cm^2) and seed mass (SM) (mg) as traits characterizing, on average, the Spanish populations of the studied species, as detailed in Martínez-Vilalta et al. (2010). Thus, we assume that these functional traits are more variable between than within species, as supported by Martínez-Vilalta et al. (2010). Trait information was mostly acquired from the Catalan Ecological and Forest Inventory (IEFC, Burriel et al. 2000–2004; http://www.creaf.uab.es/iefc/), which was performed between 1988 and 1998 and covers a range of environmental conditions comparable to those of continental Spain in terms of altitudinal and climatic gradients. The information on WD, SLA and Nmass was completed by published values following comparable methodologies (see Martínez-Vilalta et al. 2010), LA information was completed by local flora (Bolós et al. 1990), and SM was taken entirely from published sources, primarily from Spanish populations. These data sources provided reliable average information of the considered traits for the conditions found in the geographical range of the study.

An average description of the climatic conditions where each species is currently found in the considered region was estimated from the mean of some climatic parameters (obtained from Digital Climatic Atlas of the Iberian Peninsula DCAIB, Ninyerola et al. 2005; http://opengis.uab.es/wms/iberia/english/en_model.htm) corresponding to the plots

where the species was recorded: average mean annual temperature (MAT), mean annual precipitation (MAP) and mean ratio of summer (June–August) precipitation to potential evapotranspiration (P/PET). We used the standard deviations of these parameters (named MAT SD, MAP SD and P/PET SD, respectively) to characterize the climatic variability of each species' range.

2.3 Climatic suitability modelling

We estimated the projected change in climatic suitability for each species in the studied territory by comparing the average climatic suitability from 1950 to 2000, as provided by DCAIB and considered as the climate baseline, to the one projected for the period 2001–2100, as generated by the HadCM3 global circulation model (GCM) using the A1 scenario (IPCC 2007). We choose such a relatively long period for the climate change situation to stress changes on the climatic suitability of long-lived tree species. The A1 scenario considers an increase in atmospheric CO_2 to 810 ppm by 2080, with an associated increase in average temperature of 3.1 °C by 2080 for the area included in this study (in comparison to 1960–1990 period), and an average decrease in precipitation of 95 mm. We choose this relatively non-conservative scenario in order to stress changes in species vulnerability. Also, the considered combination of GCM and scenario represents a plausible situation for the Iberian Peninsula according to the current climatic trends and the ability of GCM to reproduce historical patterns.

Current climate variables were extracted from DCAIB at 200 m spatial resolution. Future climates were obtained at the same resolution by statistical downscaling of GCM grids (see Keenan et al. 2011 and Supplementary Material, Annex 2 for further information). Climatic suitability maps for each species were built from Generalized Linear Models (GLMs) based on presence/absence data of IFN3, after geographically fitting each IFN3 plot to the climatic regionalization. Given that IFN3 provided information on presence/absence, this procedure was preferred to other approaches only considering presence. Also, the GLM technique provides a balance between discrimination and calibration, an appropriate feature in our case, since we seek for changes in the probability of occurrence, in front of other highly discriminatory techniques. Presence was selected when the target species was dominant in the respective plot (the first or second most abundant species according to basal area). The IFN3 does not record the entire distribution of all species considered. This problem is minimized by the large extension of the Iberian Peninsula, with its broad range of environmental conditions, and the fact that relative suitability change was estimated rather than spatial outcomes. We built 250 replication datasets with different random selections of absence plots, keeping prevalence constant (Number of absence plots = Number of presence plots).

Stepwise GLMs were run for each replication dataset considering minimum, maximum and mean temperature and precipitation on a seasonal and yearly time scale, and water availability, computed as precipitation minus evapotranspiration (see Supplementary Material, Annex 2 for further details about model calculations). Suitability models for each species produced an output (suitability index, ranging from 0 to 1) that could be interpreted as the probability of dominance given a set of climatic parameters. Accordingly, we use the total area of the Iberian Peninsula as a surrogate of the respective species regional suitability. Although the resulting suitability outputs can be influenced by the different number of plots across species, we consider that the use of the ratio between projected future and current suitability, as well as the introduction of the respective number of plots of each species in the statistical analysis (see below) minimize this problem.

2.4 Analyses

We assessed the weight of phylogeny on the relationship between climatic suitability change and species characteristics by using phylogenetic generalized least squares (PGLS, Freckelton et al. 2002) and comparing partial least square models, both with phylogenetic effects included and without them. We assumed an Ornstein–Uhlenbeck model of character evolution (Martins and Hansen 1997). We constructed a phylogenetic tree for the study species using Phylomatic (Webb and Donogue 2005) based on the maximally resolved tree, considering all branch lengths to be set equal to 1 due to the multiple sources of information (see Martínez-Vilalta et al. 2010 for further details) (Supplementary Material, Annex 1).

We performed several PGLS analyses in which the response variables were (i) the ratio between the averages of the projected future and current values of climatic suitability for the whole territory, calculated for each species (hereafter, climatic suitability change), and (ii) the projected climatic suitability of the species, averaged over the whole territory (hereafter, projected climatic suitability). First we performed analyses separately for each species characteristic as explanatory variables. We also performed additional models including the number of plots in which the species occurs as an additional explanatory variable. Data on SLA for *Juniperus thurifera* L. were not available and this species was excluded in the analysis of this functional trait.

Additionally, we built comprehensive PGLS models of the climatic suitability change and projected climatic suitability of each species as a function of several descriptors of species characteristics, including the number of plots in which each species was present. We built models including all first-order interactions between species characteristics and we finally selected the best model according to the AIC criterion. For demographic rates, we selected RGR since it proved to be significantly correlated with the climatic suitability variables in the previous variable-by-variable analyses. Given the large number of descriptors in comparison to the number of species, we obtained integrative estimates of the climatic conditions where species are currently found and functional characteristics using the coordinates of species on the first component of three PCA ordinations: average climatic characterization resulting from a PCA ordination of MAT, MAP and P/PET; climatic amplitude characterization was obtained from a PCA ordination of MAT SD, MAP SD and P/PET SD and functional traits characterization was undertaken from a PCA ordination of Hmax, WD, SLA, Nmass, LA and SM. In this analysis, the value of SLA for *J. thurifera* was considered to be the same as in the congeneric *J. phoenicea* L., given that both species develop very similar scale-like leaves (do Amaral Franco 1986).

Whenever required, we applied logarithms or square roots to the variables to attain normality (see Tables 1 and 2). The R packages 'ape' and 'nlme' were used to perform the PGLS analyses and JMP 5.0 (SAS Insitute Inc) was used for the other analyses.

3 Results

Overall, most species tended to decrease their regional climatic suitability under the projected future climatic conditions, as observed when comparing projected and current climatic suitability (HadCM3 A1 scenario, Fig. 1). Only a few tree species showed an increase in climatic suitability. Most of these (*Quercus ilex* L., *Q. suber* L., *Pinus halepensis* Mill., *P. pinea* L., *P. pinaster* Ait.) are typically distributed in the Mediterranean region, in agreement with our first hypothesis. Nevertheless, the climatic suitability of *Sorbus*

Table 1 Relationship between climatic suitability change and species characteristics modelled using partial least squares. Number of plots (log transformed) was also included in the models as an explanatory variable, but it was never significant ($P<0.05$) and was removed when the fit of the model improved according to the AIC criterion. Significant relationships are highlighted in bold. (Coef, coefficient; Mort, mortality rate); see text for other abbreviations

	Model	Without phylogenetic effects			Including phylogenetic effects		
		AIC	Coef	P	AIC	Coef	P
Demographic	RGR	75.51	**2.003**	**0.010**	77.14	**1.864**	**0.023**
	MR	85.40	0.142	0.553	82.90	0.218	0.287
Functional	Hmax	88.98	0.028	0.359	87.78	−0.004	0.893
	WD	81.68	−0.021	0.991	79.35	−0.421	0.837
	SLA	74.42	0.146	0.619	74.84	0.122	0.745
	Nmass	81.23	1.132	0.159	80.34	0.754	0.452
	LA	85.14	0.127	0.098	84.28	0.109	0.235
	SM	87.77	0.046	0.489	85.35	0.061	0.449
Climatic	MAT	84.26	0.188	0.108	80.69	**0.219**	**0.035**
	MAT SD	80.79	1.152	0.104	80.21	0.792	0.221
	MAP	95.29	0.001	0.255	92.33	<0.001	0.864
	MAP SD	93.13	0.003	0.232	92.58	0.001	0.619
	P/PET	84.21	−0.179	0.989	82.10	−0.226	0.640
	P/PET SD	77.26	8.59	0.179	75.55	**15.331**	**0.003**

aucuparia L., a widespread European species that lives in mountain ranges of the Iberian Peninsula, also increased. The species with lower projected future climatic suitability are Gymnosperms of the *Juniperus* genus and trees that typically have northern distribution centers (*Fagus sylvatica* L., *Pinus sylvestris* L., *Ilex aquifolium* L.).

In agreement with to our second hypothesis, climatic suitability change correlated positively with current RGR, irrespective of phylogeny (Table 1, Fig. 2). *Pinus sylvestris* and, to a lesser extent, *P. nigra* Arnold, evade this general trend to some degree by showing a greater decrease in climatic suitability than expected from their current RGR. This correspondence between suitability change and growth concurs with a positive relationship between projected climatic suitability and species RGR (Table 2). In contrast with the expectation of coincident patterns of current demographic rates and climate tendency, mortality rate did not show any significant relationship with climatic suitability change or projected future climatic suitability (Tables 1 and 2). Similarly, functional traits failed to show any significant relationship with climate suitability change and projected climatic suitability (Tables 1 and 2).

After accounting for the phylogenetic effect, as hypothesized, there was a strong positive relationship between the range of climatic conditions where species are currently found, estimated by P/PET SD, and the climatic suitability change (Table 1). This pattern was not reflected in a significant relationship between this estimate of current species climatic range and projected climatic suitability (Table 2). Moreover, species living in localities with higher MAT are expected to experience more climatic suitability changes, resulting in an increase in their projected climatic suitability, with and without considering phylogenetic effects (Tables 1 and 2). Accordingly, species currently living in localities with higher P/PET showed lower projected average suitability (Table 2).

Table 2 Relationship between projected climatic suitability and species characteristics modelled using partial least squares. Number of plots (log transformed) was also included in the models as an explanatory variable but was removed when the fit of the model improved according to the AIC criterion. Significant relationships are highlighted in bold. See Table 1 and text for a description of abbreviations

| | | Without phylogenetic effects | | | | | Including phylogenetic effects | | | | |
| | | | Species characteristics | | Number of plots | | | Species characteristics | | Number of plots | |
	Model	AIC	Coef	P	Coef	P	AIC	Coef	P	Coef	P
Demographic	RGR	91.68	**2.565**	**0.015**			89.51	**2.388**	**0.028**		
	MR	97.81	0.177	0.535	**0.459**	**0.016**	96.43	0.234	0.382	0.400	0.052
Functional	Hmax	101.84	−0.023	0.543	**0.463**	**0.016**	99.00	−0.062	0.126		
	WD	93.18	2.103	0.332	**0.439**	**0.017**	91.60	2.200	0.404		
	SLA	89.82	0.212	0.615	**0.485**	**0.011**	88.83	0.078	0.988	**0.412**	**0.023**
	Nmass	94.60	1.034	0.307	**0.415**	**0.012**	94.09	0.438	0.713	0.369	0.660
	LA	98.66	0.124	0.199	**0.482**	**0.010**	98.37	0.088	0.425	**0.396**	**0.046**
	SM	100.15	0.141	0.107			97.32	0.124	0.300		
Climatic	MAT	83.77	**0.490**	**<0.001**			80.37	**0.456**	**<0.001**		
	MAT SD	93.93	1.222	0.160	**0.455**	**0.012**	93.67	0.936	0.260	**0.404**	**0.039**
	MAP	109.25	−<0.001	0.993	**0.433**	**0.029**	106.5	−<0.001	0.201		
	MAP SD	106.22	0.003	0.374	**0.456**	**0.014**	105.87	0.001	0.665	0.379	0.056
	P/PET	89.95	**−1.725**	**0.003**			83.83	**−1.885**	**<0.001**		
	P/PET SD	90.56	7.680	0.366	**0.499**	**0.013**	89.92	5.475	0.514	**0.427**	**0.048**

The current species abundance in the territory, estimated by the number of plots on which the species is found, did not correlate with climatic suitability change, but it did correlate positively with projected climatic suitability. This effect was clear for most demographic, functional and climate characteristics when the phylogenetic effect was not considered. When including phylogenetic effects, the effect of the number of plots remained significant only in the models of some functional traits (SLA, LA) and estimators of the climatic amplitude (MAT SD, P/PET SD) (Table 2).

In the average climate PCA ordination, species living in more arid conditions correspond to more negative values in the first ordination axis (PCA_{clim}); in the climatic amplitude PCA, species found across a wider range of climatic conditions tend to have more positive values in the first axis (PCA_{amp}), and in the functional trait PCA, species with higher LA, SLA and Nmass had more positive values in the first ordination axis (PCA_{trait}) (Supplementary Material, Annex 3, 4, 5).

When analyzing the PGLS models that considered the several descriptors of species characteristics (RGR, PCA_{clim}, PCA_{amp}, PCA_{trait}, and number of plots), the best-fitting model for species suitability change and projected suitability included RGR, PCA_{clim} and PCA_{amp} (Table 3). RGR was positively related to both suitability change and projected suitability. The relationship of the suitability variables with PCA_{clim} was negative, indicating better performance by species currently living in more arid climates, while the relationship with PCA_{amp} was positive, pointing to a better response from species living under a wider range of climatic conditions. Interactions between species characteristics were not significant and were removed from the model, along with the
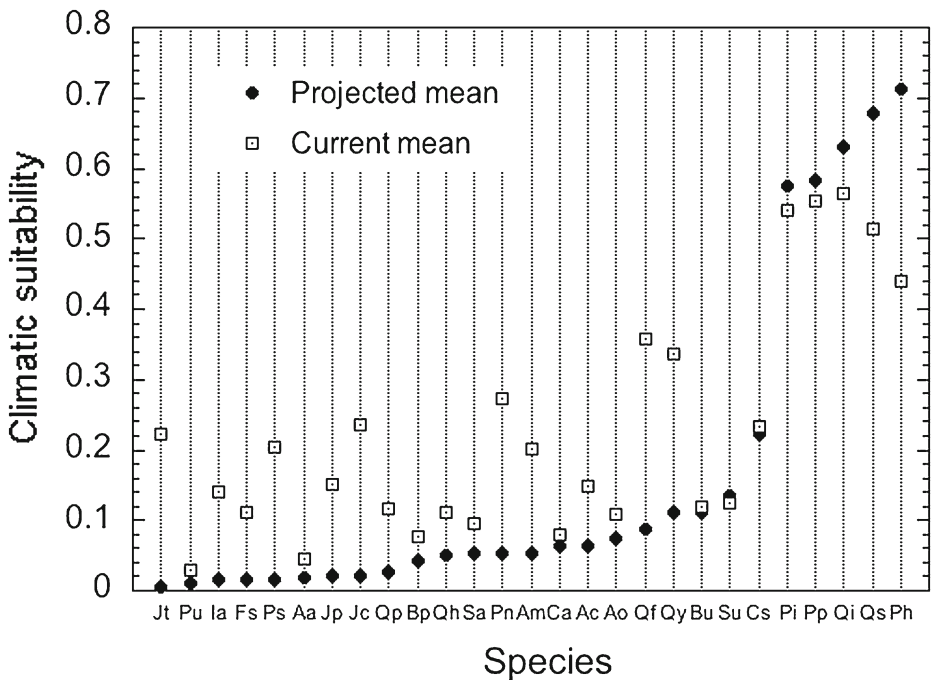
Fig. 1 Average for the whole territory of the projected future and the current climatic suitability for the 27 studied species. Aa, *Abies alba*; Am, *Acer monspessulanus;* Ac, *Acer campestris*; Ao, *Acer opalus*; Bp, *Betula pendula*; Bu, *Betula pubescens*; Ca, *Corylus avellana*; Cs, *Castanea sativa*; Fs, *Fagus sylvatica*; Ia, *Ilex aquifolium*; Jc, *Juniperus communis*; Jp, *Juniperus phoenicea*; Jt, *Juniperus thurifera*; Ph, *Pinus halepensis*; Pi, *Pinus pinea*; Pn, *Pinus nigra*; Pp, *Pinus pinaster*; Ps, *Pinus sylvestris*; Pu, *Pinus uncinata*; Qf, *Quercus faginea*; Qh, *Quercus humilis*; Qi, *Quercus ilex*; Qp, *Quercus petraea*; Qs, *Quercus suber*; Qy, *Quercus pyrenaica*; Sa, *Sorbus aria*; Su, *Sorbus aucuparia*

number of plots and the PCA ordination of functional traits. The same result was obtained when including phylogenetic effects, but the fitting of this model was slightly worse than that of models without phylogenetic effects.

4 Discussion

We did not find a significant relationship between current mortality rates and projected values of change in climatic suitability in the studied territory. Tree mortality is associated to a variety of interacting factors, which may result in a weak relationship between mortality and climatic tendency at the temporal scale considered. In fact, management and land use history may play an even more significant role on demographic rates than climate (Martínez-Vilalta et al. 2012). Thus, the set of conditions where the species can live that are described by species distribution models may not be fully recorded by presence locations, hence overestimating climatic risk (Schwartz 2012). Nevertheless, our result suggests that increasing climatic vulnerability would not exacerbate current trends of species mortality, independently of their causes. There are increasing reports of climate-related tree mortality (van Mantgem et al. 2009) specifically associated with extreme climatic episodes (Allen et al. 2010; Galiano et al. 2010). In many cases, these events may not result in
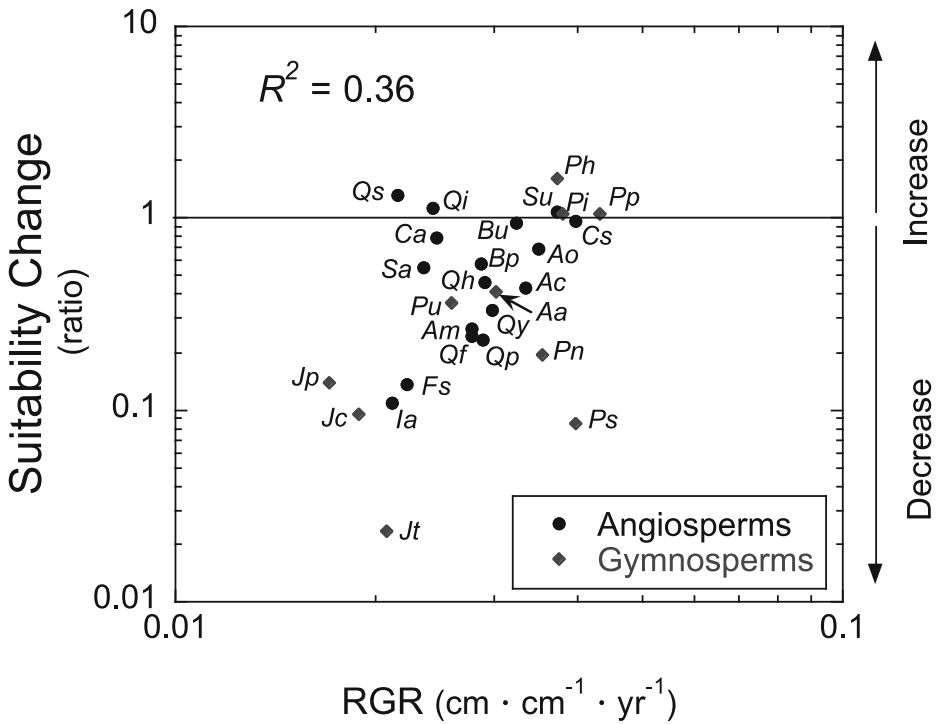
Fig. 2 Relationship between climatic suitability change and relative growth rate (RGR) for the 27 studied species. Note that axes are logarithmic. Species abbreviations as in Fig. 1

long-term changes in vegetation, suggesting that forests show important inertia to shift (Lloret et al. 2012). Although this study does not aim to discriminate the effect of such climatic anomalies, our results support the existence of drivers other than climate contributing to such inertia at a decadal scale.

Table 3 Summary of the PGLS models (best fitted model according to the AIC criterion) analyzing the climate suitability change and projected climatic suitability in relation to species characteristics. Variables describing climatic species characteristics correspond to the species values in the first axis of PCA ordinations (see text). RGR was log-transformed

	Climatic suitability change				Projected climatic suitability			
	Without phylogenetic effects		Including phylogenetic effects		Without phylogenetic effects		Including phylogenetic effects	
	AIC=78.79		AIC=80.79		AIC=76.15		AIC=77.45	
Fixed effect	Coef.	P	Coef.	P	Coef.	P	Coef.	P
Intercept	5.167	0.042	5.175	0.042	5.094	0.034	5.277	0.041
Relative growth rate (RGR)	1.725	0.017	1.727	0.017	2.195	0.002	2.236	0.003
Climate average (PCA first axis)	−0.237	0.085	−0.234	0.090	−0.763	<0.001	−0.720	<0.001
Climate amplitude (PCA first axis)	0.393	0.025	0.389	0.020	0.560	0.001	0.462	0.004

Nevertheless, our results indicate some degree of demographic vulnerability, since those species that currently present lower growth rates are more prone to experience a loss of average climatic suitability. This is the case with *F. sylvatica*, which has one of its southern edges of distribution in humid areas in the Iberian peninsula (Jump et al. 2008). *Juniperus thurifera* also exhibits a large reduction of its climatic suitability but this result may be due to an underestimation in the distribution model resulting from its limited competitive capacity (Gómez-Aparicio et al. 2011) and its history of strong control by livestock browsing (De Soto et al. 2010). Contrarily, species with current higher growth rates, such as Mediterranean pines (*P. halepensis*, which is a common colonist of secondary successions, and *P. pinaster* and *P. pinea*, which are frequently managed) experience an increase in climatic suitability in the territory.

There are, however, species that diverge from the overall positive relationship between growth and suitability change. Typical evergreen Mediterranean oaks (*Q. ilex*, *Q. suber*) with relatively low growth rates associated with water-deficit conditions are projected to increase their climatic suitability, in agreement with their expansion during the warmer conditions of the Holocene (Ramil-Rego et al. 1998; Carrion 2000). In contrast, the climatic suitability of *P. sylvestris* is expected to decrease dramatically (reflecting the location of the Iberian populations in the southwestern limit of this species' distribution) even though it exhibits relatively high growth rates. This is probably because its populations have been extensively managed for forest exploitation and they mostly consist of young stands (Vilà-Cabrera et al. 2011). These results agree with climate-driven die-off episodes that are being observed in this species (Bigler et al. 2006; Galiano et al. 2010).

Functional traits are known to correlate to some extent with current climatic conditions (Thuiller et al. 2010; Martínez-Vilalta et al. 2010) but, contrary to our expectations, they failed to correlate with the change and projection of climatic suitability in our models, probably because average values of functional traits do not account for the variability over large territories and thus for the ability of a species to adjust to spatial and temporal variability in environmental conditions (Thuiller et al. 2010), particularly in the studied region (Sabate et al. 2002). Accordingly, some recent work has called for the explicit inclusion of intraspecific variability in functional traits in studies of community ecology (Albert et al. 2011). Also, increasing CO_2 emissions is an important source on uncertainty on species response to climate change due to its direct effects on physiological performance (Keenan et al. 2011). Furthermore, most current models cannot satisfactorily evaluate the potential role of acute climatic fluctuations in species distribution (but see Zimmerman et al. 2009). However, the combination of niche-based and process-based models can provide insights about the relevance of extreme climatic variability on future patterns of species distribution (Morin and Thuiller 2009; Keenan et al. 2011). Finally, our models do not account for other factors determining species dominance and distribution, such as landscape structure and human impact, including forest management and plantation. The consequence should be a dilution of the role of autoecological features in interpreting their correspondence with climate.

The conditions where species are currently found were related to the projected change in suitability and, as hypothesized, the loss of habitat suitability would be lower for species growing in warmer habitats. Nevertheless, as for functional traits, the scarcity of significant relationships may be explained by the existence of factors other than climate that explain the current distribution of species. Climatic amplitude, particularly P/PET SD, is the best predictor of suitability change. As hypothesized, species able to successfully grow in a wide range of water deficit conditions would be less vulnerable to the new climatic scenarios.

Current regional abundance is not consistently associated with changes in climatic suitability, indicating that there is no strong bias in our estimates due to sample size. Overall,

this result supports the role of refugia in a changing climate scenario, but the climatic suitability of some rare species would diminish in the territory, as is the case of *A. alba* Mill. or *I. aquifolium*, which are more likely to be restricted by summer water deficits. Furthermore, the inclusion of phylogenetic affinity between species improves our univariate models. This trend is explained by the constraints imposed by phylogeny on species traits, and it suggests that sets of species belonging to closely related lineages might be particularly vulnerable or resilient to climate change.

This study confirms that the extrapolation to future climatic scenarios of species performance based on current patterns of dominance distribution is also constrained by factors other than species autoecology. In addition to biotic interactions and dispersal, land use and forest management should be particularly relevant for population trends (Gómez-Aparicio et al. 2011; Martínez-Vilalta et al. 2012). Also, species distribution models assume a set of biological and methodological simplifications than accumulate uncertainty to the resulting predictions (Thuiller 2004; Schwartz 2012). The relationship between the characteristics of tree species and the response of those species to future climate change may be described better by considering both the biological and historical factors.

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