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Dispersal limitation and spatial scale affect model based projections of *Pinus uncinata* response to climate change in the Pyrenees

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Abstract

Species Distribution Models (SDMs) were employed to assess the potential impact of climate change on the distribution of *Pinus uncinata* in the Pyrenees, where it is the dominant tree species in subalpine forest and alpine tree lines. Predicting forest response to climate change is a challenging task in mountain regions but also a conservation priority. We examined the potential impact of spatial scale on SDM projections by conducting all analyses at four spatial resolutions. We further examined the potential effect of dispersal constraints by applying a threshold distance of maximal advancement derived from a spatially explicit, individual-based simulation model of tree line dynamics. Under current conditions, SDM*s* including climatic factors related to stress or growth limitation performed best. These models were then employed to project *P. uncinata* distribution under two emission scenarios, using data generated from several regional climate models. At the end of this century, *P. uncinata* is expected to migrate northward and upward, occupying habitat currently inhabited by alpine plant species. However, consideration of dispersal limitation and/or changing the spatial resolution of the analysis modified the assessment of climate change impact on mountain ecosystems, especially in the case of estimates of colonization and extinction at the regional scale. Our study highlights the need to improve the characterization of biological processes within SDMs, as well as to consider simultaneously different scales when assessing potential habitat loss under future climate conditions.

Keywords: climate change, dispersal limitation, *Pinus uncinata*, Pyrenees, Species Distribution Models (SDMs)

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Introduction

Mountains are one of the most important areas in terms of endemic diversity at the global scale, but they also constitute one of the most vulnerable areas to climate change because they experience sharp climatic, topographic, and ecological changes at small spatial scales (Körner, 2003). Recent tropospheric warming has resulted in a variety of responses, including in some cases an upward shift in the position of alpine tree lines (Diaz *et al.*, 2003; Parmesan, 2006; Harsch *et al.*, 2009; Harsch & Bader, 2011). If high mountain forests ascend, upslope habitat may shrink and thereby push some alpine plant species to extinction (Parmesan, 2006; Dirnböck *et al.*, 2011). As a consequence, there is a growing interest in predicting future changes in forest distribution. A common approach to address this issue relies on empirically derived statistical relationships between environmental variables, including current climate conditions and species occurrence data (Elith *et al.*, 2010). Such statistical Species Distributional Models (SDMs) are then used to project changes in species distributions using climate data generated by complex, atmosphere-ocean general circulation models (AOGCMs), a kind of data widely available thanks to the shared efforts of UN IPCC (e.g. IPCC, 2007).

The complex topography characteristic of mountain ecosystems, such as the ecotones between subalpine forests and alpine grasslands poses two main limitations to the SDM based approach. First, current AOGCMs are usually run with the aim of projecting future climate at coarser spatial scales of hundreds of kilometers (e.g. Trenberth, 1992). In this way, they usually provide a raw representation of features like mountain ranges and land-ocean boundaries. This characteristic makes that their output cannot be reliably applied to regional scales, a spatial context which is

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regarded to be the most appropriate to predict species responses in mountain areas (Guisan & Zimmermann, 2000). Nevertheless, recent advances in AOGCM downscaling using Regional Climate Models (RCMs) have solved this issue to some extent (Christensen *et al.*, 2007b). The second limitation is that the scales considered in training SDMs are commonly too coarse for mountain specific features like alpine tree lines, i.e. complex ecotones with characteristic scales of the order of hundreds of meters (Holtmeier, 2009). In many cases, information obtained from small areas is aggregated at larger scales, even if after this process they no longer represent the scale of the processes expected to play a role in determining species distributions (Burke *et al.*, 1991; Jelinski & Wu, 1996; Dark & Bram, 2007). At the same time, and like any other kind of statistical analyses in a spatial or temporal context, SDMs are compromised by the grain size selected. Thus, the potential influence of the spatial grain or scale on the results should be explored (Openshaw & Taylor, 1979; Jelinski & Wu, 1996; Dark & Bram, 2007; Trivedi *et al.*, 2008; Randin *et al.*, 2009; Seo *et al.*, 2009).

A third major caveat of the SDM approach, although not an exclusive one of studies focusing on mountain species, is their inability to incorporate biological processes like species interactions, Allee effects or spatial population dynamics (Guisan & Thuiller, 2005; Jeltsch *et al.*, 2008; Elith *et al.*, 2010). For example, ignoring dispersal limitation is commonly highlighted as one of the major weaknesses of SDMs (Engler *et al.*, 2009; Willis *et al.*, 2009). Dispersal limitation has been demonstrated to play an important role in constraining potential species migration under rapidly changing environmental conditions, even in the case of highly mobile species (Araújo & Rahbek, 2006). Thus, predictions based on SDMs should be complemented with insights derived from dynamic and spatially explicit population models. In the case of the dynamics of mountain forest ecosystems, individual-based models are ideally suited to perform this task, given the small scales involved and the potential importance of spatial and stochastic effects (Dullinger *et al.*, 2004; Martínez *et al.*, 2011).

In the Pyrenees, *Pinus uncinata* forms dense subalpine forests, and it is the main component of alpine tree line ecotones (Ninot *et al.*, 2007; Améztegui *et al.*, 2010). An upward migration of this species would seriously threaten alpine plant species currently inhabiting habitat available upslope (Parmesan, 2006). Despite no shifts in tree line position have been detected, both field (Camarero & Gutiérrez, 1999, 2004; Tardif *et al.*, 2003; Batllori & Gutiérrez, 2008) and modeling (Benito Garzón *et al.*, 2007, 2008; Montoya *et al.*, 2009; Mezquida *et al.*, 2010) studies have highlighted different responses of this species to recent climate warming and the importance of climatic factors in determining its current and past distribution. Here, we examine the potential impact of climate change on *P. uncinata* distribution across the Pyrenean range (i.e. Andorra, France, and Spain). At the same time, we take advantage of this system to check the potential impact of scale-dependence and of dynamic processes such as dispersal limitation in the context of the SDM approach. To this end, we fitted SDMs considering a set of environmental variables corresponding to different hypotheses on factors governing *P. uncinata* distribution to range maps of different spatial resolutions. On the basis of the output from RCMs, we used the fitted SDMs to project the expected *P. uncinata* distribution at the end of this century. These projections were then combined to create ensemble projected distributions under different climate change scenarios. Finally, we combined results from an individual-based model with SDM based projections to constraint the potential migration of *P. uncinata*. Our study reveals potential impacts of varying scale and dispersal limitation on the assessment of climate change impacts on mountain forest ecosystems, and highlights potential threats to alpine flora in the Pyrenean range.

Material and methods

Study species and area

The *P. uncinata* Ramond ex DC is a long-lived, slow-growing, and shade-intolerant conifer, which reaches its south-western distributional limit in the Iberian Peninsula (Ceballos y Fernández de Córdoba & Ruiz de la Torre, 1979). In the Pyrenees, this species forms forests between *c.* 1700 m and *c.* 2300 m a.s.l., and it dominates most of the alpine tree line ecotones on any substrate and at any exposure (Ninot *et al.*, 2007). Potential tree line elevation reaches between 2100 and 2450 m in the Pyrenees, depending on continentality, exposure, and land-form (Cantegrel, 1983; Gil Pelegrín & Villar Pérez, 1988; Carreras *et al.*, 1996).

The Pyrenees are a mountain range elongated from West to East which covers the Iberian Peninsula isthmus. The northern and eastern slopes are more pronounced than the southern and western slopes where the elevation gradient is smoother. Substrates are granitic and gneiss in origin in the eastern Pyrenees, whereas calcite becomes more common westward and southward. Soils are in general poorly developed or rocky and acidic, especially in zones inhabited by *P. uncinata* (Cantegrel, 1983). The climate of the Pyrenees is strongly conditioned by its proximity both to the Atlantic Ocean and the Mediterranean Sea, which influence temperature regimes at both ends of the range (Del Barrio *et al.*, 1990). Autumn and winter storms cross the isthmus predominately from the Bay of Biscay, discharging on the western and central Pyrenees by orographic lifting, and causing a rain shadow at the eastern part where conditions are in general drier. In this way, the north-western area is regarded as part of the Atlantic biogeographical region where the forest limit is dominated by deciduous species, like *Fagus sylvatica.*

During the second half of the last century *P. uncinata* forests have not been greatly affected by human disturbances (i.e. grazing, logging). Before this, historical data indicates moderate human exploitation during the eighteenth century (García-Ruiz, 1988; estimated a 30% coverage of farmlands below 1600 m), and in the early twentieth century farms and other settlements were moved to the bottom of valleys. Aerial photographs (1946, 1957, and 1990) and dendroecological analyses at some alpine *P. uncinata* tree lines in the central Pyrenees indicate no upward shifts (Camarero & Gutiérrez, 1999, 2004; Batllori & Gutiérrez, 2008; Batllori *et al.*, 2010). Indeed, a detailed analysis comparing aerial photographs (1956, 2006) of the Eastern Pyrenees (Catalonia) suggests that *P. uncinata* has expanded its distributional range mainly in the lowermost forested areas, recolonizing previously logged or grazed areas (Améztegui *et al.*, 2010).

Here, we studied *P. uncinata* distribution in an area covering the entire Pyrenean range (19 386.9 km^2, Fig. 1), considering Spanish and French ranges (no data was available for Andorra). Distributional maps of *P. uncinata* were retrieved from the Third Spanish Forest Inventory (Tercer Inventario Forestal Nacional, IFN3, 1997–2007, scale 1 : 50 000) and from the French Forest Inventory (Carte Forestière version 1, 1994–2001, scale 1 : 25 000). These maps provide locations where *P. uncinata* ranked at least third in terms of areal coverage, using parcels of varying size depending on local characteristics (minimum parcel size 2.5 ha). To examine the effect of scale, we processed these data using a set of four nested grids of squared cells varying in resolution from 200 m to 1600 m, defining each cell overlapping with a parcel occupied by *P. uncinata* as a presence. The minimum resolution chosen guarantees an appropriate integration of the two data sources employed. An equal amount of cells where the species was not found was defined as true absences within a 10 km radius from the mapped distribution at each scale, to train different models using a balanced dataset (Liu *et al.*, 2005).

Environmental variables

A set of seven topographic and climatic predictors were selected to represent different hypotheses about environmental conditions constraining *P. uncinata* distribution (Table 1). To include topographic effects, slope and aspect were extracted from a satellite derived digital elevation model (DEM) (Table 1). To represent the effect of climatic factors, we considered both mean precipitation during the driest month (June; P_6), a proxy of water deficit; and mean temperature of the coldest month (February; T_2), which conditions winter survival of trees (Körner, 2003; Batllori *et al.*, 2009). On the other hand, recent analyses of tree ring data indicated that warmer conditions in the Pyrenees might increase *P. uncinata* radial growth. Specifically, warm conditions during autumn (November), before tree-ring formation and during the spring (May), when the tree grows, are the main predictors of individual tree growth (Tardif *et al.*, 2003). Therefore, including mean temperature in November (T_{11}) and mean temperature and precipitation in May (T_5, P_5) as additional predictors

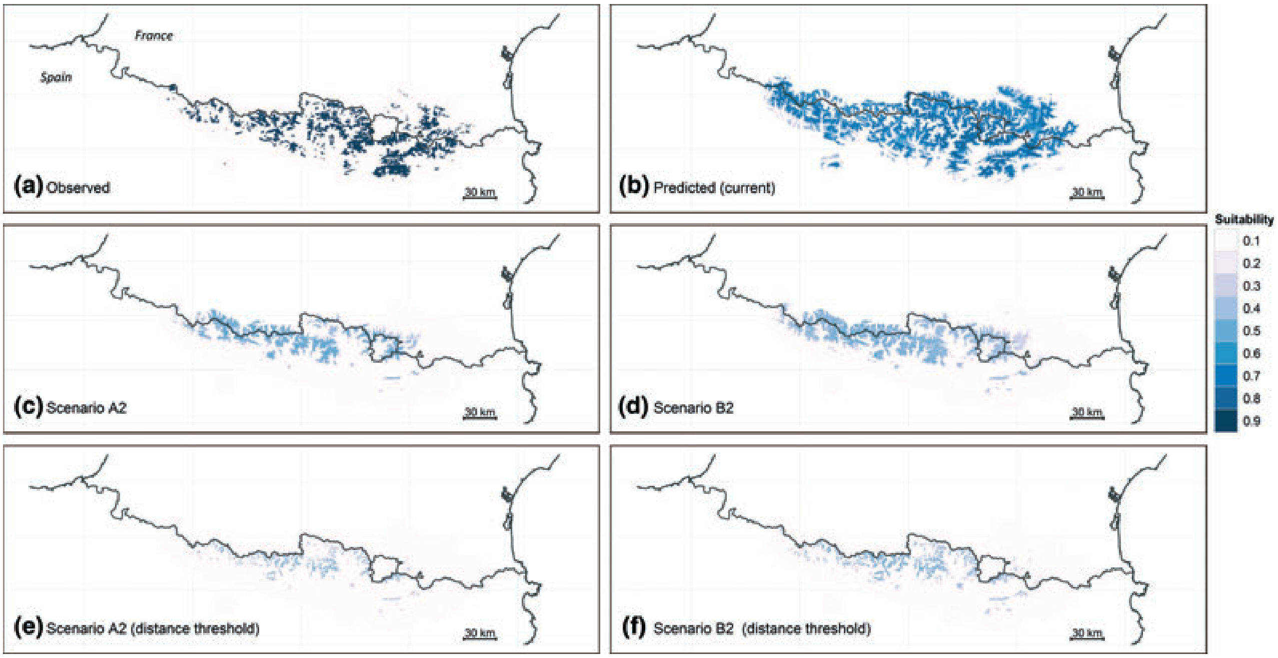

Fig. 1 Maps of P. *uncinata* observed and projected distribution. Suitability maps were produced under two different climate change scenarios (A2 and B2) before and after considering the effect dispersal limitation, included through a dispersal distance threshold based on simulations of an individual-based model (see *Dispersal limitation*). All maps were produced at the finer resolution employed in the study (200 × 200 m^2).

Table 1 Environmental variables employed in the GAM analyses; (below) list of the Regional Climatic Models available as part of the PRUDENCE project. See text for further details.

Variables	Original resolution	Source or Reference
P. uncinata distribution	50 m	Tercer Inventario Forestal Nacional (IFN3, Spain) (http://www.marm.es)Inventaire Forestier National (France) (http://www.ifn.fr/spip/)
Topographic variables Slope Aspect	30 m	ASTER GDEM (http://www.gdem.aster.ersdac.or.jp/), Fujisada *et al.* (2005)
Climatic variables Temperature Precipitation	30 m	Global Historical Climatology Network (http://www.ncdc.noaa.gov/ghcnm/)Peterson & Vose (1997)
Regional Climatic Models ARPEGE, HIRHAM, HadRM3P, RegCM (3), RCAO, PROMES	25–50 km	PRUDENCE project (http://prudence.dmi.dk) (Christensen *et al.*, 2007a)

might account for the potential constraining effect of individual tree growth on *P. uncinata* distribution.

Temperature and precipitation data between 1960 and 1990 were obtained from meteorological stations throughout the Pyrenees (n = 121 and 173 for temperature and precipitation, respectively). These data were used to create a monthly climatology based on time series of maps estimated using universal kriging, which included the effect of elevation and a polynomial trend on location coordinates (Cressie, 1993; analyses were performed using the *R* package fields by Furrer *et al.*, 2010). Environmental variables were first calculated for the smallest grain employed in the study (i.e. 200×200 m^2), and then integrated to lower resolutions except in the case of aspect, which was derived separately from DEMs of different resolutions.

Future temperature and precipitation conditions were derived from regional downscaled climate model simulations available as part of the PRUDENCE project (Christensen *et al.*, 2007a). We used simulation results from six RCMs (Table 1) for the A2 (a scenario with high greenhouse gas (GHG) emissions and a very heterogeneous world) and B2 (a scenario with lower GHG emissions and a world focused on local environmental sustainability) IPCC climate change scenarios (SRES, Nakicenovic *et al.*, 2000; IPCC, 2007). The six RCMs have a resolution between 25 and 50 km and incorporate an improved representation of the effects of topography on climate, an issue of especial relevance for the region under study. Mean climate conditions predicted from each regional climate model were derived for two time periods: 1960–1990 and 2070–2100. The difference in mean temperatures and the ratio between mean precipitations during each period was then calculated and interpolated using ordinary kriging. Increments were preferred over absolute values because of their greater spatial smoothness. These maps were finally combined with climatologies estimated from meteorological station data (see above) to project future conditions. Finally we extracted for each of the twelve climatic scenarios the five climatic variables (i.e. T_2, T_5, T_{11}, P_5, P_6) at the different spatial scales to project the distribution of *P. uncinata*.

Dispersal limitation

The inability to incorporate dispersal limitation is commonly highlighted as one of the main weakness of SDMs (Jeltsch *et al.*, 2008; Engler *et al.*, 2009). One promising approach is to combine statistical SDMs and spatially explicit plant population models, like individual-based models. We took advantage of a recently parameterized individual-based model that describes *P. uncinata* tree line dynamics (Wiegand *et al.*, 2006; Martínez *et al.*, 2011) to estimate a potential distance threshold for *P. uncinata* expansion. The tree line model considers basic demographic processes and interactions like competition, facilitation, and dispersal limitation, with rules based on empirical studies conducted at Pyrenean tree line ecotones, i.e. the transition areas from the subalpine closed forest to the treeless alpine vegetation which includes the uppermost trees with a minimum height of 2 m (Camarero & Gutiérrez, 1999, 2004; Batllori & Gutiérrez, 2008; Batllori *et al.*, 2010). The model was able to reproduce a variety of real tree line physiognomies from gradual to abrupt or krummholz tree lines, which emerged when nonlinear responses in individual rates of growth or mortality with respect to the altitudinal gradient were considered (Martínez *et al.*, 2011).

We used the best parameterizations of the models (n = 100) obtained for the site Tessó (42° 36′ N, 01° 03′ E, 2330–2360 m a.s.l.) that included growth and mortality gradients, and constraints in seed dispersal. The Tessó tree line can be regarded as representative for most of the Pyrenean undisturbed alpine tree lines with gradual height decrease upslope and without krummholz. The models were run until the steady state was reached (i.e. adult density stabilized), resulting in tree lines with properties similar to those found in the field. Then, we allowed simulations to continue for 90 years (i.e. from 2010 until 2100) after removing constraints on individual growth and mortality with altitude. We thus released the external constraints typical for tree lines to represent a transition to fully benign environmental conditions. With this configuration, *P. uncinata* expansion within the modeling arena is only constrained by population dynamics and dispersal limitation, allowing us to set an upper bound on rates of forest migration upslope. To retrieve a conservative estimate of potential dispersal, we recorded the uppermost position of adult upright trees in each simulation. This sample of distances was fitted to a lognormal distribution to estimate the 95th percentile, which was set as the distance threshold (P_{95} = 1358.14 m). In this way, we obtained a distance threshold which was used to assess potential constraints due to dispersal limitation and population dynamics in *P. uncinata* expansion under future climate conditions.

Statistical analyses

A set of correlative SDM for *P. uncinata* was fitted to presence–absence maps of varying resolution in the Pyrenees. We included topographic as well as climatic effects on growth and survival by considering different environmental variables (see *Environmental variables*). Nonlinear relationships are commonly found when examining environmental constraints on species distributions, so the ability to handle this kind of relations is a desirable feature of SDMs.

Here, we employed Generalized Additive Models (GAM; e.g. Hastie & Tibshirani, 1990; Wood, 2006), a method widely used in SDMs (Guisan & Zimmermann, 2000) to identify the most important environmental factors needed to describe the distribution of *P. uncinata* in the Pyrenees and, based on this knowledge, to project future changes in response to global climate change. Given the binary nature of presence-absence data, we used a *logit* link function to model observed binary probabilities in terms of a linear predictor combining both unspecified smooth functions of the predictor variables and conventional linear relationships. All the models were fitted in *R* (*R Development Core Team,* 2010) using the implementation of GAMs in the package *mgcv* (Wood, 2008). In this package, the relationship between environmental variables and binary probabilities of presence is determined using thin plate regression splines with a degree of smoothness determined by generalized cross-validation.

The influence of each covariate was assessed first separately and later in combination with other covariates to represent different hypotheses on topographic constraints, climatic stress, and growth limitation (Table 2). However, we excluded combinations where two variables showed strong collinearity (i.e. $r > 0.8$). Model quality was assessed employing the k-fold cross-validation ($k = 10$) value of two metrics; the Area Under the receiver operating characteristic Curve (AUC), and the Hanssen-Kuiper Skill Score or True Skill Statistic (TSS). We based model selection on TSS values because of its known ability to provide good results in classification problems (Hastie *et al.*, 2009) and because it provides a reliable assessment of the predictive ability of different models (Allouche *et al.*, 2006). We also included the results of model selection based on the Akaike Information Criterion (AIC), which balances model fit and model complexity (Burnham & Anderson, 2002). The AUC measures the ability of model predictions to discern observed absences and presences, without considering the absolute value of model predictions. Although some weaknesses of this metric have been recently highlighted (Lobo *et al.*, 2008), we reported AUC values because it has been widely used and because it still remains a useful metric to rank a set of models (Elith & Graham, 2009). On the basis of the TSS ranking we selected the models to project the future distribution of *P. uncinata* in the Pyrenees at year 2100 using climate data derived from RCMs. Projections from the best ranked models were averaged using the relative TSS values as weights.

Present and future *P. uncinata* distributions were compared by estimating the area which was colonized (i.e. transition from absence to presence) or became extinct; and the change in mean altitude and latitude integrated throughout the study area. Both the observed and the predicted current ranges were compared with model projections under future climate change scenarios. Because our training data set was balanced, we employed the $P > 0.5$ criterion to convert model predictions of habitat suitability to expected presences (Liu *et al.*, 2005; Jiménez-Valverde & Lobo, 2007). All indexes were estimated at each scale, but we also considered cells above and below 2200 m separately to explore potential differences in *P. uncinata* response at lower altitudes and above the alpine tree line. The high elevation zone is of special conservation interest because *P. uncinata* expansion can be considered as a potential threat to neighboring alpine vegetation (Camarero & Gutiérrez, 2002). The area colonized was standardized with respect to the area available (i.e. unoccupied cells), whereas the percentage of area that became extinct was estimated with respect to *P. uncinata* current extent.

Results

Environmental predictors of current P. uncinata *distribution*

The area estimated to be occupied by *P. uncinata* from its mapped distribution decreased with scale, ranging from 6292.48 km^2 (lattice of 1600 m in cell side) to 2965.16 km^2 (lattice of 200 m). In most cases, GAMs resulted in good fits, with AUC and TSS values well above the random expectation (i.e. AUC = 0.5 and TSS = 0; Table 2). Model predictions matched the observed distribution, but the extent of the range was overestimated in the northwestern part of the Pyrenean range, an area actually dominated by deciduous species (Fig. 1A and B). At all spatial scales, climatic factors, especially monthly mean temperatures, were the best individual predictors of *P. uncinata* distribution, whereas topographic factors provided in general a poorer fit (mean AUC of 0.81 vs. 0.57, respectively, Table 2). The strength of the effect of environmental covariates, as well as the ranking of different model structures was similar among scales in terms of AUC, TSS (Table 2), and AIC (Table S1 in the Supporting Information). Model performance decreased at coarser resolutions for models including climatic predictors, but showed an inverse pattern for topographic predictors.

Table 2 Different hypothesis on factors governing P. *uncinata* distribution in the Pyrenees and the measurements of model quality (AUC, TSS) of the corresponding models for the different spatial scales examined. High AUC and TSS values correspond to better fits. All AUC and TSS values were significantly different from their random expectation ($P < 0.01$, permutation test, $N = 100$), except in the case of the model $\alpha + f(\text{Aspect})$. Models highlighted in boldface were selected to project the future distribution of P. *uncinata*

		AUC				TSS			
		Lattice scale (m)				Lattice scale (m)			
Hypothesis	Models	200	400	800	1600	200	400	800	1600
topography	$logit(Y) = \alpha + f(Slope)$	0.56	0.60	0.65	0.63	0.05	0.12	0.17	0.06
topography	$logit(Y) = \alpha + f(Aspect)$	0.54	0.53	0.52	0.57	0.00	0.00	0.00	0.00
growth limitation	$logit(Y) = \alpha + f(T_{11})$	0.82	0.83	0.83	0.77	0.50	0.52	0.50	0.38
growth limitation	$logit(Y) = \alpha + f(T_5)$	0.81	0.83	0.82	0.77	0.49	0.52	0.49	0.37
growth limitation	$logit(Y) = \alpha + f(P_5)$	0.67	0.68	0.69	0.62	0.25	0.21	0.26	0.05
stress	$logit(Y) = \alpha + f(P_6)$	0.71	0.70	0.76	0.67	0.31	0.29	0.35	0.20
stress	$logit(Y) = \alpha + f(T_2)$	0.82	0.83	0.83	0.77	0.50	0.52	0.51	0.37
topography	$logit(Y) = \alpha + f(Slope) + f(Aspect)$	0.57	0.61	0.65	0.65	0.06	0.13	0.17	0.06
growth limitation	$logit(Y) = \alpha + f(T_5) + f(P_5)$	0.83	0.85	0.83	0.81	0.50	0.54	0.50	0.40
growth limitation	$logit(Y) = \alpha + f(T_{11}) + f(P_5)$	0.83	0.85	0.83	0.81	0.50	0.54	0.50	0.41
stress	$logit(Y) = \alpha + f(T_2) + f(P_6)$	0.83	0.84	0.85	0.79	0.51	0.53	0.53	0.40
topography + growth limitation	$logit(Y) = \alpha + f(Slope) + f(Aspect) + f(T_5) + f(P_5)$	0.83	0.85	0.83	0.82	0.50	0.54	0.51	0.45
topography + growth limitation	$logit(Y) = \alpha + f(Slope) + f(Aspect) + f(T_{11}) + f(P_5)$	**0.83**	**0.85**	**0.84**	**0.82**	**0.51**	**0.54**	**0.51**	**0.45**
topography + stress	$logit(Y) = \alpha + f(Slope) + f(Aspect) + f(T_2) + f(P_6)$	**0.84**	**0.84**	**0.85**	**0.80**	**0.52**	**0.53**	**0.53**	**0.41**

Models considering the stress or growth limitation hypothesis received similar support, with AUC values over 0.83 (Table 2). The inclusion of topographic predictors in these models resulted in a slight improvement of model fit. The two models with the highest TSS score at any scale were selected for predicting the effect of climate change on *P. uncinata* distribution. These models combined topographic factors (slope, aspect), with either climatic variables expected to enhance growth (T_{11}, P_5,) or increase stress (T_2, P_6) (Table 2).

Forecasted climatic conditions in the Pyrenees

Based on climate model projections, temperature will increase and precipitation will be likely reduced for the end of this century across the Pyrenean range. Under the A2 scenario, which assumes higher GHG emissions, climate projections resulted in an expected increase in +3.9 °C in mean annual temperature in the Pyrenean range. Higher increases were found in central Pyrenees, whereas lower increases were forecasted at the extremes of the range probably because of the tempering effect of nearby sea (Supporting Information, Fig. S1). Mean annual precipitation was expected to decrease 22.7% along the entire range, with higher decreases in the eastern Pyrenees (Fig. S1). The B2 scenario, which prioritizes local sustainability, yielded a mean increase in annual temperature of +2.9 °C and a reduction of 15.4% in annual precipitation, following a similar spatial pattern than the A2 scenario. In both scenarios, changes in temperature and precipitation were slightly more pronounced at higher elevations.

Projected changes in P. uncinata *distribution*

The comparison of observed *P. uncinata* distribution with ensemble SDM projections highlighted strong changes in the expected distribution under future climate change scenarios (Fig. 1). The area occupied by *P. uncinata* in future projections was reduced in most cases with respect to its present distributional range, an effect stressed at coarser resolutions. As expected, the reduction was more pronounced for the A2 scenario, where projected *P. uncinata* ranges were reduced to 67.6% (59.5–76.9) (mean and range among scales) of its current extent. On the other hand, projections for the B2 scenario resulted in a much lower decrease in *P. uncinata* extent which even turned to a small increase at the highest resolution considered [i.e. current extent reduced to 95.7% (85.4–106.5)]. These changes increased when constraints in dispersal were considered, resulting in a 28.2% (26.7–30.2) reduction in the area projected to be occupied by *P. uncinata* for the A2 scenario, and a 39.4% (38.3–42.1) for the B2 scenario. At the same time, scale effects nearly vanished when dispersal constraints were considered, resulting in similar predictions among scales (i.e. note the reduced ranges among scales in the expected percentage of reduction).

We found an upward migration in the habitat potentially suitable for the focal species, a response which was consistent among scales, with higher displacements at finer resolutions. Such upward shift was more pronounced in the A2 scenario [572.8 m (505.0–618.9)] than in the B2 scenario [436.0 m (381.0–471.8)] [difference A2 minus B2: 136.8 m (123.9–147.1)]. A similar pattern was found for the northward displacement of the mean latitudinal range [A2 scenario, 16.0 km (14.4–17.2) vs. B2 scenario, 15.7 km (13.5–17.3)], although differences between scenarios were small [A2 vs. B2: 0.3 km (−0.2–0.9)]. Taking into consideration dispersal constraints slightly increased the estimates of forest migration upslope under the A2 [583.6 m (516.4–633.8)] and B2 scenarios [442.7 m (389.6–476.9)], and in mean latitude [A2, 16.1 km (14.7–17.2) vs. B2, 16.1 km (14.3–17.7)].

The net reduction in the habitat occupied by *P. uncinata* in future projections was the result of colonization (i.e. new suitable areas) and extinction processes (formerly suitable areas that became unsuitable) along its altitudinal range (Fig. 2). Colonization and extinction showed also different responses depending on the emission scenarios and the scale considered. In the case of colonization, both the area and especially the percentage estimated to be occupied increased at coarser resolutions [Fig. 2; A2, 2148.8 km^2 (2078.2–2216.7) vs. B2, 2669.8 km^2 (2454.2–2795.9)]. The percentage of area colonized in alpine areas (i.e. above 2200 m) was higher for the A2 scenario, whereas the colonization of areas below 2200 m was most important in the B2 scenario (Fig. 2). A similar pattern was detected after applying constraints in dispersal, although in this case less area was colonized [A2, 1095.4 km^2 (982.6–1163.9); vs. B2, 1289.1 km^2 (1142.7–1376.5)]. On the other hand, extinctions were predicted to occur mainly at lower locations [3247.6 km^2 (2496.6–4111.1)], whereas, as expected, the area lost at upper locations remained very low [61.7 km^2 (56.2–72.1)]. An important effect of scale was also observed, with a great increase in the percentage of area extinct at finer resolutions (Fig. 2). When the projected distribution was compared against the potential habitat available predicted by SDM for current conditions, results were quite similar (Supporting Information, Fig. S2) except for the lower estimates of colonization at elevations below 2200 m. This finding reinforces the observation that our models overestimate *P. uncinata* prevalence at lower elevations, but it is consistent with studies indicating that these zones have been historically more affected by human activities.

Discussion

The distribution of forests has changed during Earth history in response to environmental changes, demonstrating their potential ability to cope with climate

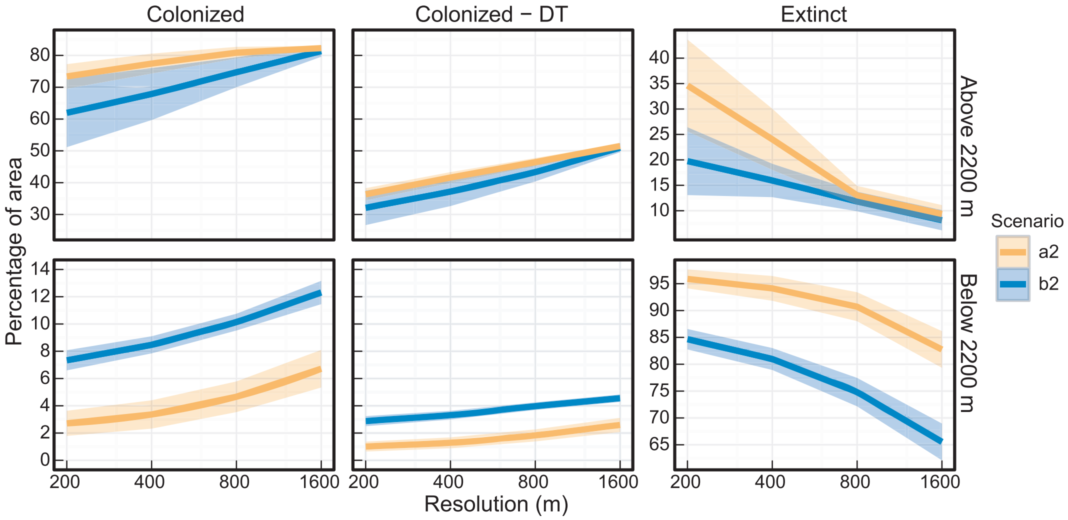

Fig. 2 Effect of spatial resolution on estimates of *P. uncinata* colonization and extinction at the end of the 21st century in the Pyrenean range. Percentages of area colonized were estimated with respect to the area available at each resolution, whereas the percentages of area extinct were estimated with respect to the area currently occupied by *P. uncinata*. Two different climate change scenarios (A2 and B2) were considered. The effect of dispersal limitation was included through a dispersal distance threshold (DT) based on simulations of an individual-based model. Estimates are provided for zones above and below the approximate elevation of the tree line (taken as 2200 m). The line and the shaded area correspond to the mean and standard error of ensemble projections from six regional climate models. Note the different scaling of the *y*-axis.

changes (Clark *et al*., 1998). However, the temporal scale of current warming is much more rapid than past climatic changes (IPCC, 2007). In this sense, current climate change may create new climates and produce no-analog or completely new forest communities (Williams & Jackson, 2007; Williams *et al*., 2007). This sets an urgent need to develop methods that are able to project potential forest migration, a daunting task in the case of mountain regions (Guisan & Zimmermann, 2000; Parmesan, 2006; Engler *et al*., 2009; Zimmermann *et al*., 2009). Here, we have assessed the potential distribution under global climate change for the dominant tree species in subalpine forests and alpine tree lines in the Pyrenees. To this end, we combined SDMs, the output from RCMs, and estimates of potential tree migration derived from a spatially explicit and individual-based simulation model of *P. uncinata* tree line dynamics.

In general, we found that the current distribution of *P. uncinata* can be well described by SDMs including climatic predictors, especially mean temperatures at critical times during the seasonal cycle, as expected from previous observational (Camarero & Gutiérrez, 1999, 2004; Tardif *et al*., 2003; Batllori & Gutiérrez, 2008) and modeling studies (Benito Garzón *et al*., 2007, 2008; Montoya *et al*., 2009; Mezquida *et al*., 2010). Models representing either stress or growth limitation conditions received a similar support. Based on climate model projections from downscaled, RCMs (Christensen *et al*., 2007b), warmer and drier conditions can be expected for the end of this century across the Pyrenean range. In general, future projections under two contrasting emission scenarios (A2 and B2) resulted in a considerable decrease in the areas potentially suitable for *P. uncinata*, with a net migration of a few hundred meters upslope in their mean elevation of their potential range. After considering constraints of dispersal and population dynamics, the extent of projected distributions was reduced and the area that could be potentially colonized nearly halved. Also, the responses observed varied depending on the scale considered to describe the distributional range, especially when different climate change scenarios were compared. In the following, we discuss the effect of changing observational scale and incorporating dispersal limitation in projecting the future response of alpine tree lines to climate change, to end with some considerations regarding the expected future impacts in the Pyrenean range. Before that, we underline some of the caveats and uncertainties related to the approach employed in this study.

One of the main assumptions of SDMs is that they rely on a presumed static equilibrium between observed range distributions and environmental conditions, an assumption which can be too restrictive in the context of highly dynamic environments like mountain ecosystems (Guisan & Zimmermann, 2000). Recent phylogeographic evidence indicates the existence of multiple *P. uncinata* glacial refugia in the Iberian Peninsula (Heuertz *et al*., 2010), so we can expect a minor impact of postglacial dispersal limitation in its current distribution. On the other hand, Améztegui *et al*. (2010) have highlighted recent *P. uncinata* encroachment and potential recolonization of low-elevation locations previously used by human assemblages for cattle grazing in the eastern Pyrenees. This would have altered to some extent our characterization of *P. uncinata* realized lower tolerance limits for climatic variables. Nevertheless, we expect that, to some extent, the high prevalence of *P. uncinata* at lower elevations (e.g. a quarter of the observed range was below 1574 m) can compensate for human alterations of its current distributional range, and indeed false positives were common at lower elevation zones (Fig. 1). This was reinforced by analyses conducted considering only data on protected areas, such as National Parks (not shown), which resulted in models of the realized niche very similar to those reported here.

Although we can expect a reasonable characterization of the realized niche of *P. uncinata* in terms of physiological constraints, at least at the latitudinal rear edge of its distribution, biological interactions may also influence species distributions and their response to climate change (MacArthur, 1972). In the Pyrenees, forests at mid elevations are dominated by *F. sylvatica* L., *Pinus sylvestris* L. or deciduous *Quercus* sp. These species are also expected to migrate upslope under milder conditions (e.g. Peñuelas *et al*., 2007; Benito Garzón *et al*., 2008), where they would probably outcompete *P. uncinata*. At the leading front or at the uppermost forest limits, we expect our approach to be more reliable despite ignoring biological interactions, given the predominance of positive interactions in harsh environments upward (Callaway, 1998). Under the milder conditions brought by climate warming, the importance of facilitation processes might be reduced. Nevertheless, the inclusion of interactions with other tree species at both the uppermost and lowermost limits is a desirable feature for future studies (Baselga & Araújo, 2009; Willis *et al*., 2009).

Dispersal plays an essential role in determining the degree of correspondence between tree species distribution and climate conditions (Clark *et al*., 1998). Indeed, including this process in SDMs has been identified as one of the greatest challenges for the projections of species responses to climate change (Elith *et al*., 2010). Previous studies have highlighted that climate change might surpass the ability of tree species to cope with habitat migration (Iverson *et al*., 2004). Here, we used estimates of population expansion derived from a detailed individual-based model to constrain SDM projections. Incorporating these constraints into model predictions resulted in dramatic changes in the amount of area potentially suitable to be colonized by *P. uncinata*, but only in slight changes in estimates of altitudinal and latitudinal migration. Scale effects on estimates of the percentage reduction in *P. uncinata* total extent nearly disappeared after considering dispersal constraints. Similar approaches can be easily applied in other study systems and, even with limited knowledge on the ecology of the focal species, a variety of methods are available for the estimation of population dispersal rates (e.g. Clark *et al.*, 2003; McLachlan *et al.*, 2005). Indeed, the dispersal rates provided by the individual-based model were consistent with those provided for other *Pinus* sp. in the literature (e.g. Clark *et al.*, 2003). Nevertheless, our estimates were based only on model parameterizations derived for one representative tree line, and variation among different localities might condition future migration. For example, it is expected that abrupt tree lines or tree lines with krummholz may expand less than diffuse tree lines (Harsch *et al.*, 2009). At the same time, our individual-based model ignored interannual variability in environmental conditions which are known to determine recruitment success in *P. uncinata* (Camarero & Gutiérrez, 2004; Batllori *et al.*, 2009), a process which might ultimately determine local rates of migration. In any case, the results presented here clearly illustrate the need to account for dispersal limitation in SDMs (Jeltsch *et al.*, 2008), which can be important even when preparing the training dataset (Václavík & Meentemeyer, 2009). Interestingly, dispersal limitation had only limited importance for shaping tree line patterns on local scales (Martínez *et al.*, 2011), indicating the existence of a scale transition from which dispersal begins to be limiting for tree recruitment. For instance, attending to projected impacts on alpine vegetation, estimates of the habitat potentially suitable upslope ignoring dispersal limitation would provide figures doubling those expected when dispersal constraints are taken into account.

Another source of uncertainty revealed by our study was the spatial resolution used for modeling species distributions. Although the effect of environmental covariates was in general consistent between scales, we detected a slight change in the importance of topographic and climatic variables. These and even more pronounced effects are commonly found when different scales are assessed (see Jelinski & Wu, 1996). We also found a consistent overestimation of both the percentage and the total area colonized at coarser resolutions, whereas the opposite effect was found in the percentage of suitable habitat lost. The net balance was dominated by colonization, with a reduction in the percentage of current extent predicted to be lost under future climatic conditions at finer resolutions. This is in agreement with what would be expected under the so called local 'refugia' hypothesis, i.e. SDMs might overestimate overall extinction if they miss small scale refugia as well as the new areas that might become suitable for colonization (Randin *et al.*, 2009). After considering dispersal constraints, differences among scales in the percentage reduction in *P. uncinata* total extent nearly vanished. These results reflect both the nonlinear nature of the effect of spatial scale on the estimation of quantities like rates of habitat clearance, as well as the interaction of scale effects with dispersal constraints. It is thus desirable that future SDM studies continue examining the potential effects of spatial homogenization and aggregation on projected changes in species distribution in response to climate change. Similar effects are common in geographical ecology and have been found in the context of reserve planning and landscape analysis (Openshaw & Taylor, 1979; Jelinski & Wu, 1996; Dark & Bram, 2007; Seo *et al.*, 2009), although the scales considered in SDM studies (e.g. kilometers) are usually far from those employed in landscape planning (e.g. a few hundred of meters or less).

The impacts of climate change on mountain ecosystems are expected to be apparent in the forthcoming decades (Körner, 2003; Parmesan, 2006; Dirnböck *et al.*, 2011). Here, we found that under two contrasting climate change scenarios, *P. uncinata*, the main component of alpine tree line ecotones in the Pyrenees, is expected to migrate northward and upward, occupying habitat currently inhabited by alpine plant species. We found nevertheless that, when current approaches based on SDMs are employed, either the consideration of dispersal limitation or changing observational scales can modify the assessment of climate change impact on mountain ecosystems. In this way, our study highlights the need to improve the characterization of biological processes within SDMs, as well as to consider simultaneously different scales when assessing potential habitat loss under future climate conditions. These are necessary steps to meet the social requirement of preserving the high biological diversity and to maintain the valuable ecosystem services (water management and erosion prevention) hosted by mountain forest ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Future temperature and precipitation conditions at the 21st century for the climate change scenarios A2 and B2.
Figure S2. Effect of spatial resolution on estimates of P. *uncinata* colonization and extinction at the end of the 21st century in the Pyrenean range.
Table S1. Different hypothesis on factors governing P. *uncinata* distribution in the Pyrenees and additional measurements of model quality of the corresponding models for the different spatial scales examined.