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ORIGINAL ARTICLE

Drastic reduction in the potential habitats for alpine and subalpine vegetation in the Pyrenees due to twenty-first-century climate change

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Abstract Recent climate change is already affecting both ecosystems and the organisms that inhabit them, with mountains and their associated biota being particularly vulnerable. Due to the high conservation value of mountain ecosystems, reliable science-based information is needed to implement additional conservation efforts in order to ensure their future. This paper examines how climate change might impact on the distribution of the main alpine and subalpine vegetation in terms of losses of suitable area in the Oriental Pyrenees. The algorithm of maximum entropy (Maxent) was used to relate current environmental conditions (climate, topography, geological properties) to present data for the studied vegetation units, and time and space projections were subsequently carried out considering climate change predictions for the years 2020, 2050 and 2080. All models predicted rising altitude trends for all studied vegetation units. Moreover, the analysis of future trends under different climate scenarios for 2080 suggests an average loss in potential ranges of 92.3–99.9 % for alpine grasslands, 76.8–98.4 % for subalpine (and alpine) scrublands and 68.8–96.1 % for subalpine forest. The drastic reduction in the potential distribution areas for alpine grasslands, subalpine scrublands and *Pinus uncinata* forests highlights the potential severity of the effects of climate change on vegetation in the highest regions of the Pyrenees. Thus, alpine grasslands can be expected to become relegated to refuge areas (summit areas), with their current range being taken over by subalpine scrublands. Furthermore, subalpine forest units will probably become displaced and will occupy areas that currently present subalpine scrub vegetation.

Keywords Alpine grasslands · Climate change · Maxent · *Pinus uncinata* forest · Pyrenees · Subalpine shrubs

Introduction

Recent climate change is already affecting both ecosystems and the organisms that inhabit them (Walther et al. 2002; Parmesan 2006; Rosenzweig et al. 2008), with mountains and their associated biota being particularly vulnerable to climate change (Beniston et al. 1996; Theurillat and Guisan 2001). In fact, it has been noted that plants of alpine and subalpine areas appear to be especially sensitive to global warming (Shaw et al. 2000; Erschbamer 2001; Pauli et al. 2001). Moreover, it is likely that such effects are more intense in mountain systems under extreme and climatically marginal conditions (Beniston 2000), such as in many alpine areas with a Mediterranean climate influence, in which most of the orophilous species are relicts from glacial periods and are considered at the limit of their climatic tolerance range (Sanz-Elorza et al. 2003). Furthermore, impacts on flora from regions projected to undergo increased warming accompanied by decreased precipitation, such as the Pyrenees, will likely be greater than those on flora in regions

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where the increase in temperature is less pronounced and rainfall increases concomitantly (Engler et al. 2011).

In the last two decades, species- and community-based models have been increasingly used in conservation planning, and more recently, they have become important tools to evaluate the potential impacts of climate change on biodiversity (Guisan and Zimmermann 2000; Thomas et al. 2004; Guisan and Thuiller 2005; Ferrier and Guisan 2006). Concerning the former, species distribution models (SDMs) generate species' potential distributions in landscapes based on the relationship between species observations (presence/absence or abundance) and environmental variables. Regarding community-based models, two major approaches currently prevail (Guisan and Rahbek 2011). The first approach focuses directly on realized properties of species assemblages and uses macroecological modelling. The second approach focuses on aggregate properties of individual constituent species, used to reveal the properties of assemblage, and applies SDMs to a spatial stack of species (S-SDMs). Many studies have modelled the potential areas of species in the future under climate change scenarios of the intergovernmental panel on climate change (IPCC), but the work carried out by Thomas et al. (2004) was one of the first studies to apply SDMs to the problematic of climate change impact on organism geographic distribution for a large number of species. In Europe, the greatest modelling effort was carried out by Engler et al. (2011), who assessed the possible effects of climate change on the potential distributions of 2,632 plant species by the end of the twenty-first century in all major European mountain ranges at a fine spatial resolution (100 m; 1 km for the Spanish Pyrenees). However, most studies in Europe have focused on modelling species presence at the continental scale at a resolution of 50 × 50 km (Bakkenes et al. 2002; Thuiller et al. 2005) using input data taken from the Atlas Florae Europaeae (Jalas and Suominen 1972–1996). Other regional approaches have been applied for the Swiss Alps (Bolliger et al. 2000; Dirnböck et al. 2003; Walther et al. 2005; Pauli et al. 2007) and for 20 tree species on the Iberian Peninsula (Benito Garzón et al. 2008). Effects of ongoing climate warming on alpine plant species distribution have already been detected in several Iberian mountain ranges (Peñuelas and Boada 2003; Sanz-Elorza et al. 2003; Benito et al. 2011). Specially, Benito et al. (2011) pointed out that the suitable areas for species inhabiting the summits of Sierra Nevada (SE Iberian Peninsula) may disappear before the middle of the century. Thus, according to these studies, the alpine and subalpine vegetation in the Pyrenees can be expected to suffer similar trends as a consequence of the projected climate change. Hence, we expected that the vegetation belts in the Pyrenees will suffer an upwards shift, being, thus, the alpine belts the most affected by the climate change (see Benito et al. 2011; Engler et al. 2011).

In this study, we chose to model the potential distribution of entire vegetation units (as defined in CORINE; Vigo et al. 2006) rather than individual species for the following reasons: first, although vegetation units are not as sharply and objectively defined biological entities as species, for all of the vegetation units studied in this work, the mapping at our disposal, which is based on detailed orthophoto maps and intense field work, provides continuous layers of current distributions with a planimetric accuracy much greater than what is achieved in the case of species. Furthermore, the studied vegetation units are mainly defined by the presence of the dominant or key species. The behavior of the key species will determine the survival of many accompanying species, given that the former act as a nurse plant for the latter, creating appropriate micro-niches (Castro et al. 2004). Thus, investigation of the distribution of these vegetation units is consistent with investigation of the distribution of their dominant or key species. What is more, the reduction in the area that is climatically suitable for a particular vegetation unit determines the magnitude of the extinction risk for species belonging to it (Thomas et al. 2004). Moreover, to our knowledge, no detailed study has been conducted that assesses the future of the alpine and subalpine vegetation in the Pyrenees with such planimetric accuracy (resolution of approximately 0.6 km^2) under future climatic conditions. Finally, it is important to note that the studied units have a high conservation value because seven of them are habitats of community interest and two are habitats of priority interest under the 'Habitats' Directive 97/62/UE (Council Directive 97/62/UE of October 27, 1997, adapting Directive 92/43/EEC to technical and scientific progress on the conservation of natural habitats and wild fauna and flora).

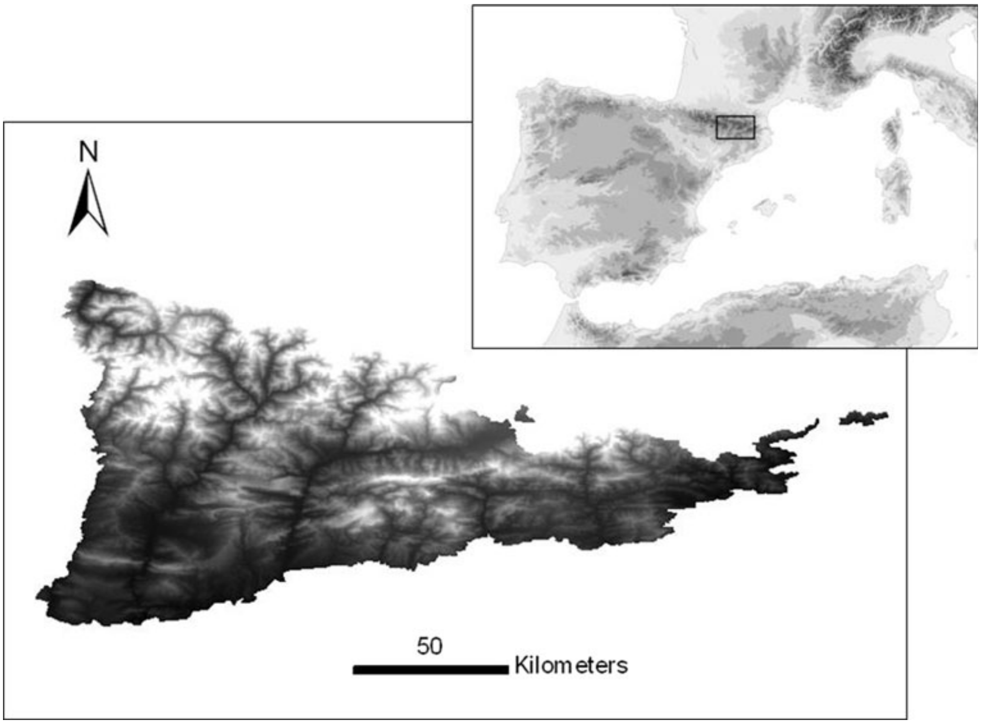
In this study, we assess the impacts of climate change on the potential distribution of six alpine grasslands, two subalpine (and alpine) scrublands and four subalpine forests of *Pinus uncinata* in the Oriental Pyrenees by the end of the twenty-first century using 700 × 900 m habitat samples and data expressing two IPCC-based climate change scenarios for the years 2020, 2050 and 2080.

Methodology

Study area

The study area covers a total area of 9,894 km^2, including the subalpine and alpine belts in the eastern half of the Spanish Pyrenees and Andorra (Fig. 1). Detailed vegetation mapping (Carreras et al. 2003; Vigo et al. 2006) and field surveys carried out mainly by Spanish botanists have provided excellent knowledge regarding the vegetation and flora in this area. In the Pyrenees, there is essentially one

Fig. 1 Map showing the location of the study area in the Oriental Pyrenees (NE Spain and Andorra)



tree species that inhabits the upper subalpine area: mountain pine (*P. uncinata*). At the tree line ecotone, open woods give way to a patchy area with small areas of dwarf scrub, grassland, tree islands and isolated trees. The vegetation above the forest limit, in the alpine zone, forms a small-scale mosaic of structurally and floristically distinct plant communities, including short grasslands clearly dominated by *Festuca eskia*, *Festuca airoides* or *Carex curvula* (on acidic substrata) and grasslands of *Kobresia myosuroides* or *Festuca gautieri* (in carbonated soils), dwarf scrub (formed by, e.g., *Rhododendron ferrugineum*, *Genista balansae*, *Vaccinium uliginosum* ssp. *microphyllum*), and sparse vegetation on rocky substrata and scree (Braun-Blanquet 1948; Carrillo and Ninot 1992). *Rhododendron* and *Genista balansae* dwarf scrub are placed on north- and south-facing slopes, respectively, and both can be either primary or secondary vegetation communities in alpine and subalpine areas severally. Traditional logging and bush burning for pasture are the main causes that explain their presence in subalpine areas as secondary vegetation communities.

Distribution data

In the Oriental Pyrenees, 57 CORINE vegetation units (legend units of the interpretation manual; Vigo et al. 2006) appear covering the surface of the alpine and subalpine belts (see Vigo et al. 2006 for further details). According to criteria such as occupation area, representativeness and ecological importance, we selected 12 of these units (Table 1) which comprise the Pyrenees' main alpine and subalpine landscapes: subalpine forest of *P. uncinata* and subalpine (and alpine) scrublands, and grasslands distributed mainly in the alpine belt. The geo-referenced distribution data for the 12 studied vegetation units were obtained from both Catalonia habitats mapping (scale 1:50,000 with a minimum area of representation of 150 × 150 m, approximately 2.25 ha), a scientific project conducted during the period 1998–2003 (Vigo et al. 2006), and Andorra habitats mapping (scale 1:25,000 and 1.6 ha resolution; Carreras et al. 2003).

However, due to the spatial accuracy of the climate maps, the study was conducted at a resolution of approximately 0.6 km^2, that is, the spatial accuracy of the climate maps dictated the resolution at which spatial projection and analyses were carried out for the study area. Hence, the habitats mapping were rasterized to a 700 × 900 m grid using ArcGis 9.3 analysis tools (ESRI 2009). Lastly, these rasterized maps were converted into points which were positioned at the centers of all cells that they represent for modelling using ArcGis 9.3 conversion tools (ESRI 2009).

Environmental data

Environmental data included 36 climate layers, five layers describing geological materials and 11 topographic layers. We represented the current climate using monthly minimum

Table 1 Studied CORINE vegetation units; test omission rates (OR) at the maximum sensitivity plus specificity threshold; AUC values; and changes in the suitable area for the 12 studied vegetation units by the year 2080 under scenarios A2 and B2, and assuming universal dispersal

Vegetation unit	OR	AUC	Current potential distribution (km^2)	A2 scenario			B2 scenario		
				Maintained (%)	Increased (%)	Reduced (%)	Maintained (%)	Increased (%)	Reduced (%)
31 g *Rhododendron ferrugineum* heaths[a]	0.048	0.935	1,377.23	0.31	0.48	98.90	8.34	6.94	74.84
31 u Subalpine and alpine *Genista balansae* formations[a]	0.051	0.950	1,102.29	0.59	3.43	95.38	9.23	19.28	55.62
36a Alpine acid snow-patch communities	0.031	0.977	529.10	0.00	0.00	100.00	0.65	0.00	92.82
36 b Alpine calcareous snow-patch communities dominated by espalier *Salix* species	0.000	0.986	682.59	0.03	0.00	99.94	2.27	0.00	92.38
36 g *Festuca eskia* garland grasslands	0.034	0.906	1,615.64	0.15	0.03	99.66	11.32	0.24	74.76
36 h Acidophile *Carex curvula* grasslands	0.026	0.981	404.85	0.00	0.00	100.00	3.25	0.61	86.98
36 i Alpine *Festuca airoides* grasslands	0.049	0.973	1,247.68	0.05	0.00	99.90	1.03	0.01	95.14
36 m Alpine calcicolous *Kobresia myosuroides* swards[a]	0.049	0.986	363.64	0.00	0.00	100.00	0.09	1.35	97.05
42 f Mesophile and acidophilus *P. uncinata* forests[a]	0.076	0.888	2,072.51	2.64	6.99	87.72	24.01	17.27	26.41
42 g Xerophile *P. uncinata* forest of siliceous adrets[a]	0.062	0.907	1,862.03	0.56	6.24	92.65	18.76	18.16	52.28
42 h Xerophile *P. uncinata* forest of calcareous adrets[b]	0.059	0.964	887.85	0.14	2.08	97.63	9.54	18.68	67.38
42 i Mesophile calcareous *P. uncinata* forests[b]	0.050	0.956	1,105.09	0.36	4.80	94.47	8.80	17.97	74.64

Areas maintained, lost and gained by 2080. All performance metrics are based on the data partition (80 % training, 20 % test) generated for each vegetation unit

[a] Habitats of community interest under the habitats directive

[b] Habitats of priority interest under the habitats directive

temperature (Tmin), monthly maximum temperature (Tmax) and monthly precipitation (Ptotal) data layers provided by the WorldClim database. These data layers are generated through the interpolation of mean monthly climate data (averaging the period corresponding to 1950–2000) from climate stations onto a 0.6 km^2 resolution grid (Hijmans et al. 2005).

The spatial biodiversity patterns in the Pyrenees are strongly influenced by topography and geological properties (Pausas et al. 2003). Based on geological maps of Catalonia (scale 1:250,000) from the Cartographic Institute of Catalonia (ICC 1996), we carried out a simplification to obtain five geological variables (carbonate materials, silicon materials, substrates with sulfate, quaternary deposits and water bodies). Then, these geological data were adapted to the reference grid, and we calculated the percentage of each cell containing each type of geological material. Additionally, topographic data were obtained from a digital elevation model of Catalonia (DEM; with a resolution of 20 × 20 m) developed from the topographic database of Catalonia at a 1:50,000 scale (ICC 2010). From this map, we calculated the maximum, minimum and average for both the altitude and the slope for each cell of the study area. Moreover, we obtained the percentages of each cell facing north, south, east, west and plane surfaces from the DEM. Finally, these data were adapted to a resolution of 700 × 900 m, allowing them to be overlaid with climate data.

To avoid multi-collinearity problems, which can result in model over-fitting (Peterson et al. 2007), we reduced the number of environmental predictors using a principal component analysis (PCA) in the software Ginkgo (version 1.7, http://biodiver.bio.ub.es/vegana/). We selected the first ten PCA axes as our environmental predictors (PCA01-10; Table S1 in Online Resources) because each of these axes separately explains more variance than would be expected by chance (1.78 %), and they jointly explain 97 % of the variance in the data.

Climate change scenarios

To simulate the distribution of the investigated vegetation units under possible future climate conditions, we used global climate model data from the IPCC third assessment report provided by the WorldClim database (http://www.worldclim.org/futdown.htm).

We used two different climate projections for the 1990–2080 time period developed by the UK Hadley Center for Climate Prediction and Research (Mitchell et al. 2004; Mitchell and Jones 2005). These were derived from a global circulation model (HadCM3; Carson 1999) and are based on two different socioeconomic scenarios proposed by the IPCC (Nakicenovic and Swart 2000): A2FI and B2FI (hereafter referred to as A2 and B2, respectively). The A2 scenario storyline describes a very heterogeneous world with a continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other scenarios. The B2 scenario describes a world in which the emphasis is on local solutions to economic, social and environmental sustainability, with a continuously increasing population (lower than A2) and intermediate economic development.

With projected average warming of +4.99 °C over our study area by 2080, the A2 projection represents the most severe climate change scenario that we considered, while B2 was the mildest (+3.58 °C). Greenhouse gas emissions from the two scenarios will affect global climate change in different ways, with A2 having a more drastic effect on vegetation compared to B2. The future climatic condition trends in the study area are shown in Fig. 2 as changes in air temperature and precipitation.

Vegetation units distribution modelling

We used Maxent (Phillips et al. 2006) version 3.3.1 to relate current environmental conditions to vegetation occurrence data (i.e., points of vegetation units' presences derived from CORINE habitats mapping) and subsequently carried out spatial and temporal projections for the two possible future climate scenarios. Maxent estimates the potential geographic distribution of studied vegetation units by finding the probability distribution of maximum entropy, or closest to uniform, subject to constraints derived from occurrence data (Phillips et al. 2006). Maxent has been found to represent a promising and robust approach for modelling species distributions in both current (Elith et al. 2006; Hernandez et al. 2006) and future environments (Hijmans and Graham 2006).

Occurrence data often exhibit a spatial bias in survey efforts, which will impact the quality of predictions (Phillips et al. 2009). However, the coverage of the vegetation units across the Oriental Pyrenees is continuous, consistent and has a good planimetric resolution, so one of the advantages of modelling these types of data over their associated species occurrences is that the sampling distribution for these vegetation units in the study region is exactly known (with much greater precision than the climate data). Before projecting the model, we applied a mask representing rocky areas to avoid projections at locations that are unsuitable, regardless of climate, topography and geological properties.

We employed recommended default parameters for this version of the model, including regularization multiplier = 1, maximum iterations = 500, convergence threshold = 0.00001 and a maximum of 10,000 background points. To evaluate the quality of the predictions under current climatic conditions, we carried out a random partitioning of the occurrence localities for each vegetation unit and divided the databases into two subsets: calibration and evaluation. The former subset, a random sample from 80 % of the total database, was used to calibrate (train) the models, whereas the latter subsample, comprising the remaining data, was used to evaluate (test) the model's predictions (Fielding and Bell 1997).

The results provided by Maxent were evaluated from the evaluation dataset (20 % of total data), employing the area under the receiver operating curve (AUC, ROC) method (Manel et al. 2001). The ROC curve characterizes the model's performance at all possible thresholds using a single number that represents the area under the curve (AUC). This procedure has been extensively used to evaluate models (Hanley and McNeil 1982; Fielding and Bell 1997). For models found to have a good predictive performance (test AUC >80 %), we projected the model from the present (1990) to each interval of 30 years until the year 2080.

Before performing migration simulations (described below), the model results were imported into ArcGis 9.3 (ESRI 2009) to produce maps of potentially suitable areas. We reclassified the probabilistic projections of each Maxent model into binary values (presence–absence grids) representing either suitable or unsuitable areas. This conversion required the selection of a threshold above which a pixel was reclassified as potentially suitable, whereas it was unsuitable below the threshold. We tested the threshold that maximizes sensitivity plus specificity under the current climate (see Liu et al. 2005; Jiménez-Valverde and Lobo 2007; Fitzpatrick et al. 2008).

Dispersal scenarios

We used three simple dispersal scenarios, universal, zero or limited dispersal, to estimate the percentage gain or loss of the geographic range for each vegetation unit. The universal dispersal scenario assumes that vegetation can

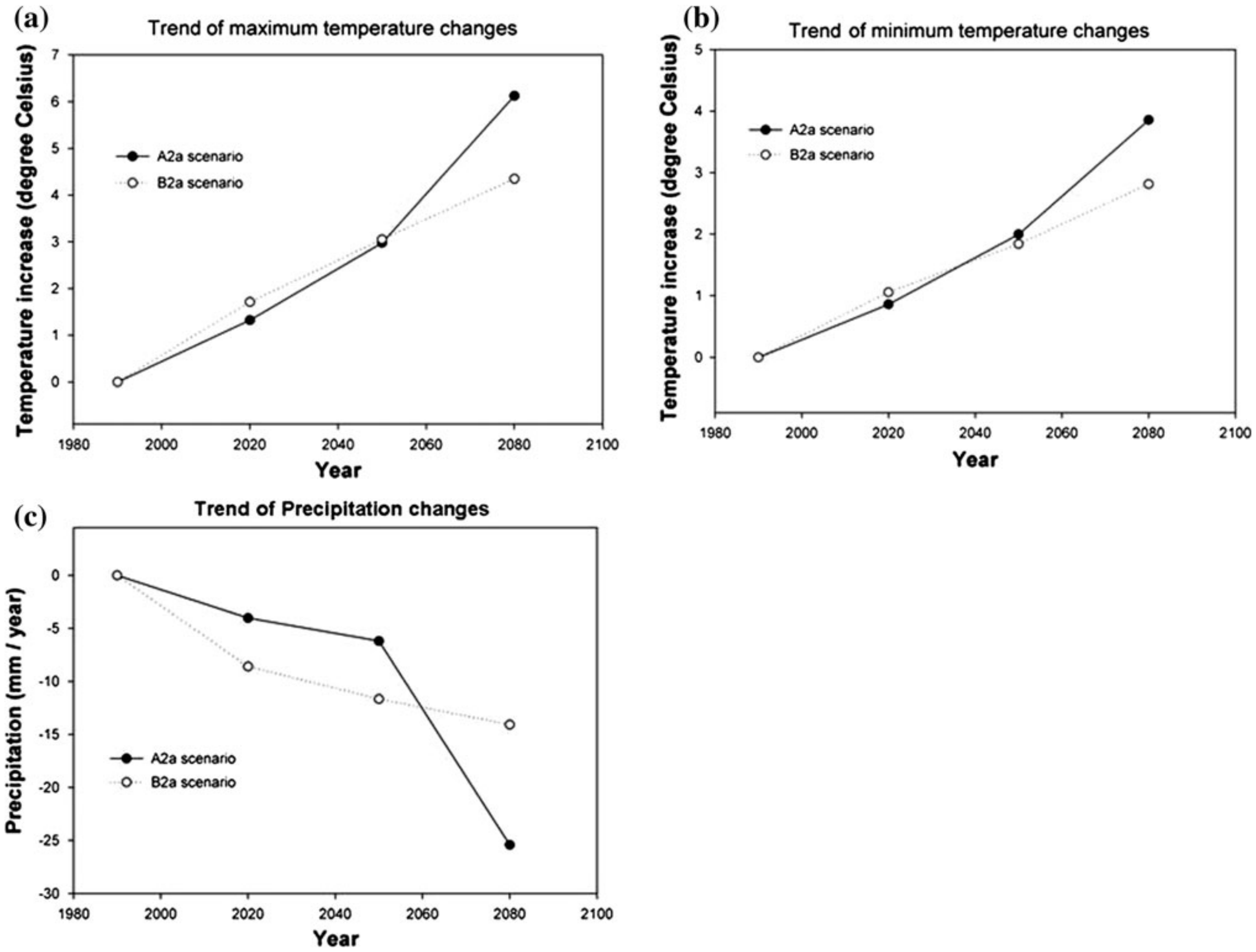


Fig. 2 Changes in the mean annual air temperature and accumulated annual mean precipitation according to the HadCM3 Global Circulation Model projected under the IPCC SRES A2 and B2 scenarios in the Spanish Pyrenees and Andorra. **a** Trend of maximum temperature changes, **b** Trend of minimum temperature changes, **c** Trend of Precipitation changes

track their shifting climate envelopes, and the future distribution of vegetation will mirror the future spatial extent and location of those environments that are suitable for them. Therefore, we are assuming that all pixels projected to become potentially suitable as a result of climate change will be occupied by the vegetation units. This assumption might be conservative (i.e., optimistic), but it has been shown to provide good estimates of species loss levels for mountain areas (Engler et al. 2009). The zero dispersal scenario assumes that vegetation will persist only in areas where the modelled current and future geographic ranges overlap. In cases where there is no overlap, vegetation units are assumed to become extinct. However, historical constraints will cause realized species ranges to fill only limited proportions of the fundamental range, which is defined as the range that would be achieved should all dispersal constraints be overcome (Gaston 2003). Thus, using the limited dispersal scenario, we quantify the extent to which vegetation units fill their current modelled climatic potential range in the study area (i.e., the capacity to occupy their full suitable area). For this objective, we computed the current realized/potential range size ratio (R/P) (Gaston 2003) across the study area, where P is the number of climatically suitable pixels defined by the Maxent model maps, and R is the number of climatically suitable pixels within the occupied distribution maps of the vegetation units. Thus, we obtained an indicator of the amount of the suitable area that was actually occupied (dispersal ability simulator). We assumed that maintained areas remain constant, and we applied this indicator to expansion areas after assuming universal dispersal. This scenario represents an intermediate dispersal scenario. We thus obtained the percentage of area lost, but we do not know where that loss occurs.

The spatial overlap between the modelled current and future vegetation presence/absence grids was calculated using ArcGis 9.3 tools (ESRI 2009) for each climate scenario and time period, producing cell counts of current and future distributions.

Changes in vegetation units' distribution

Using the predictions for each vegetation unit, the maintenance, expansion or reduction in their ranges with respect to their current potential distribution was quantified for each scenario. The maintained distribution area was predicted from the area occupied at the present time that was also expected to be occupied in the future (year 2080). Expansion was defined as the area not occupied at present that was likely to be occupied by the vegetation unit in the future. Reduction was calculated from the area occupied at present that will most likely not be occupied in the future.

Finally, we calculated both the altitudinal shifts and the potential area loss of the modelled vegetation units for the year 2080 as follows:

$$[(\mathrm{Area}_{2080} \times 100)/\mathrm{Area}_{\mathrm{current}}] - 100.$$

A unit is expected to become extinct when it is predicted to lose 100 % of its suitable area. However, because the link between area losses and extinction formally requires a population viability analysis in addition to predictions of spatial distribution analysis (Botkin et al. 2007), we only discuss our projections in terms of suitable area losses, that is, the percentage change in the size of the area.

Results

Algorithm performance

The models developed using Maxent had good to excellent predictive ability, as measured by the AUC values (Table 1). The AUC ranged from 0.888 to 0.986. The relatively high AUC values indicate that the distributions of the vegetation units are well described by the climate, topography and geological properties of the study area. Additionally, for the chosen threshold, all models showed low omission rates, indicating that only a small percentage of test points fell outside the area predicted as suitable (Table 1).

Projected distribution by 2080

Our models predict that climate change will have a substantial impact on the geographic ranges of the 12 studied vegetation units (Table 1), with the climate change severity scenario and dispersal scenario influencing the magnitude of the modelled range change responses. An increase in climate change severity (A2 scenario) increases the risk of loss of potential areas for all modelled vegetation units. Considering our results, the following trends are apparent (Table S2, and Figures S1 and S2 in Online Resource).

Alpine grasslands (vegetation units 36 in Table 1)

By 2080, the size of the area occupied by alpine grasslands was significantly reduced under the two climate scenarios, losing 99.9 % (±0.1 standard deviation) of the area of occupation on average under the conditions of the A2 scenario and 92.3 % (±7.5 standard deviation) under the conditions of the B2 scenario. For the six studied alpine grassland, assuming universal dispersal, the modelled geographic ranges decline with increasing climate change severity. When incorporating the current R/P range size ratio, or if zero dispersal is assumed, the same trends in direction occur, but declines in the modelled range size are more severe. Therefore, these vegetation units were predicted to suffer an intense and rapid reduction in their ranges (Table 1; Fig. 3a), with particularly strong effects being seen for the snow-patch communities of acid soils (36a; Figure S1c and Figure S2c in Online Resource), the grasslands of *Carex curvula* (36 h; Fig. 4; Figure S1f and Figure S2f in Online Resource) and the swards of *Kobresia myosuroides* (36 m; Figure S1h and Figure S2h in Online Resource); these are formations that appear at higher elevations and seem to show a low capacity to maintain or expand their ranges, which could lead to their extinction by the year 2080.

Regarding changes in altitudinal trends, it is expected that the studied group of alpine grasslands (group 36 in the legend for CORINE habitat mapping of Catalonia and Andorra) will rise between 310 and 415 m by the year 2080, reaching a mean altitude of 2,733 m under the A2 scenario and 2,627 m under the conditions of the B2 scenario.

Subalpine (and alpine) scrublands (vegetation units 31 in Table 1)

Our models predict a great reduction in the modelled geographic ranges of the two high mountain scrub formations by 2080, with this potential area loss being greater with increasing climate change severity and decreasing dispersal rates. For the *Rhododendron ferrugineum* heaths (31 g), the modelled geographic range declines by 98.9 % under the more severe scenario (A2) assuming universal dispersal and by 74.8 % under the B2 scenario with universal dispersal. When zero dispersal is assumed, the modelled range size for this formation decreases more dramatically, losing 99.7 % of its potential area under the A2 scenario and 91.6 % under B2. Finally, when incorporating the R/P ratio, we observe an intermediate situation, in which the loss of suitable area is 99.2 % under the conditions of the A2 scenario and 78.6 % under the less

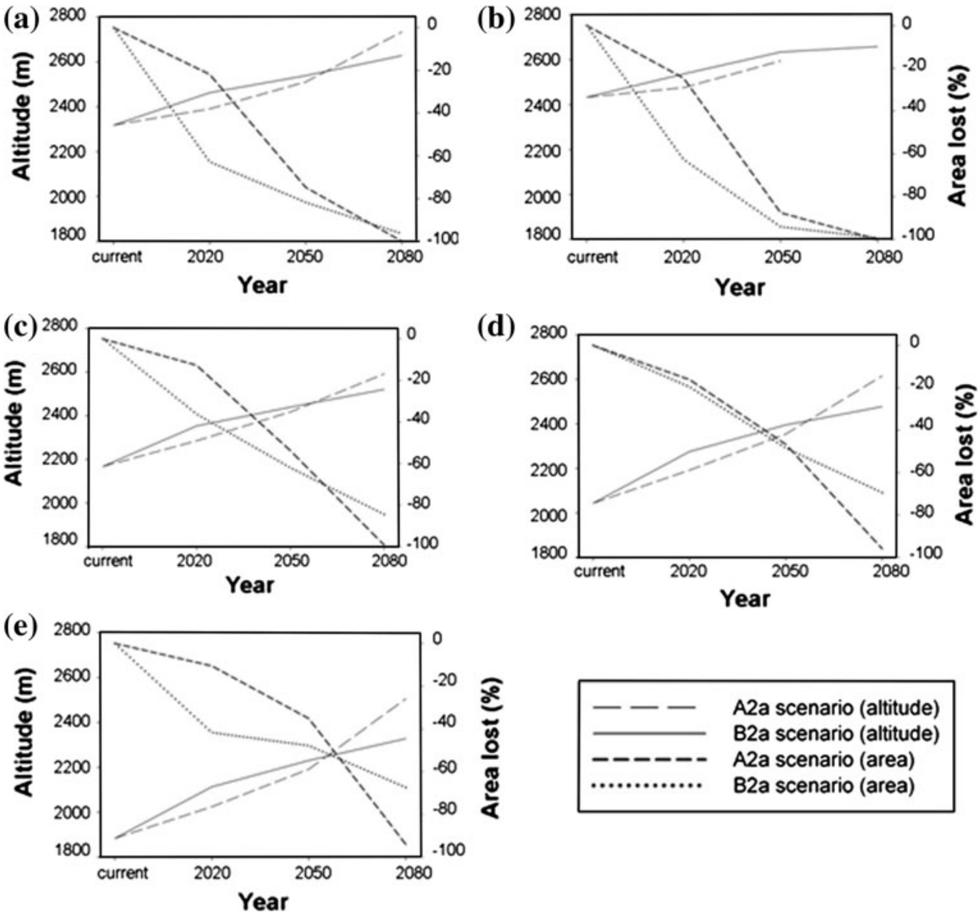


Fig. 3 Quantifying the change trends expressed as losses in the potential range and as an increase in the mean altitude for the two change scenarios assuming universal dispersal: **a** alpine grasslands (units of group 36); **b** alpine acid snow-patch communities (unit 36a); **c** *Rhododendron ferrugineum* heaths (unit 31g); **d** *Genista balansae* scrublands (unit 31u); and **e** subalpine *P. uncinata* forests (units of group 42)

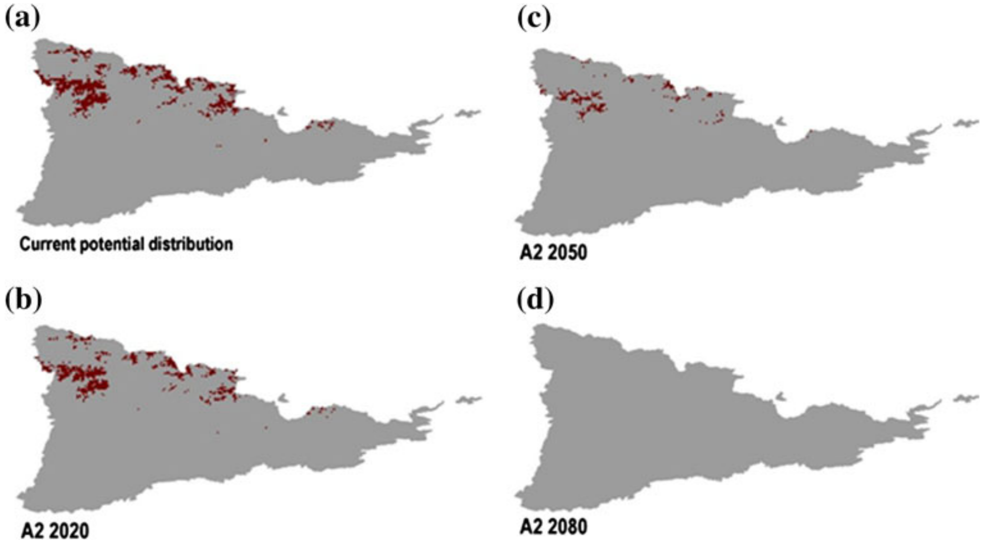


Fig. 4 Potential distribution of acidophile *Carex curvula* grassland (unit 36 h) in the present and under the climate projections of scenario A2 (2020, 2050 and 2080) assuming universal dispersal

severe scenario (B2). The *Genista balansae* formations (31u) are predicted to suffer a slightly less drastic decline, losing 95.4 % of their area by 2080 under the A2 scenario and 55.6 % under the B2 scenario assuming universal dispersal. When zero dispersal is assumed, this subalpine scrubland shows a reduction in its potential area of 99.4–90.8 % (scenarios A2 and B2, respectively). Figure 3c, d show the general trends of reduction in the ranges of these subalpine scrubs.

Regarding the changes in altitudinal trends, our results show an altitudinal increase for these subalpine scrublands of between 394 and 498 m by the year 2080, reaching an average altitude of 2,603 m under the A2 scenario and 2,500 m under the B2 scenario.

Pinus uncinata subalpine forest (vegetation units 42 in Table 1)

In general terms, our results suggest that by the year 2080, these vegetation units will present suitable occupation areas at higher altitudes than today (Fig. 3e), reaching an average altitude of 2,505 m under the A2 scenario and 2,327 m under the B2 scenario, shifting scrublands and alpine grasslands in part. These subalpine forests were generally predicted to undergo a less drastic reduction in the area occupied than any other vegetation unit analyzed in this study (Table 1), losing 96.1 % (±3.8 standard deviation) of their potential range on average by the year 2080 under the A2 scenario and 68.8 % (±21.2 standard deviation) under the B2 scenario. Specifically, when assuming universal dispersal, their average area lost is 93.1 % under the conditions of the A2 scenario and approximately 55 % under the B2 scenario. When assuming zero dispersal, the modelled range size decreases, losing 99 % of the suitable area under the A2 scenario and 84.7 % under B2. When incorporating the current R/P range size ratio, the projected potential area lost by the models varied between 96 and 66 % (scenarios A2 and B2, respectively).

This is the group of vegetation units for which we found the greatest differences in potential area loss based on the climate change scenario employed.

Vegetation unit extinction by 2080

Among the group of 12 vegetation units investigated, the percentage of units going extinct in the study area (100 % threshold) varied from 0 % (universal dispersal under B2) to 25 % (under A2). The percentage of vegetation units going quasi-extinct (i.e., units with over a 90 % decrease in distribution) varied from 91.6 % (universal dispersal under A2) to 100 % (zero dispersal under A2) and was never below 33 % (universal dispersal under B2). Extinctions are expected to occur between 2050 and 2080.

Discussion and conclusions

Credible scientific predictions of future impacts on biodiversity will be required to guide conservation planning and adaptation. Engler et al. (2011) suggest that changes in precipitation, in addition to warming, play an important role in determining the potential impacts of climate change on vegetation. Furthermore, in high mountains, the effects of global warming with regard to the biota are amplified (Benito et al. 2011). This is especially true in the Pyrenees, which are strongly influenced by the Mediterranean climate, because Mediterranean climate regions are projected to be among the most significantly affected by anthropogenic climate changes and show the highest levels of confidence in projected changes in rainfall (IPCC 2007). Models that forecast species distributions based on climatic scenarios for the twenty-first century predict a dramatic increase in these climatic trends, resulting in a massive reduction in mountain plant diversity. This is a matter of concern, as mountain ecosystems represent invaluable resources, both in terms of biodiversity and the ecosystem services they provide (Körner 2003; Viviroli and Weingartner 2004). Here, we used fine mapping scale data to assess climate change impacts on the potential distribution of alpine and subalpine vegetation units in the Oriental Pyrenees, and our results point to severe changes in the occupation area. Our models projected that many of the vegetation units analyzed in this study may be threatened by climate change. For all of the analyzed vegetation units, the projected impacts of climate change on the modelled geographic ranges differed mainly in the magnitude rather than the direction of the response across climate change severity and dispersal scenarios, with all vegetation unit ranges being projected to decline. Specifically, the trend shown in our analysis was that higher elevation vegetation is more vulnerable to area losses due to climate change than vegetation at lower elevations. The altitudinal extension of the Pyrenees allows scrublands and forest with a subalpine habitat suitability to move upward as the climate becomes warmer and drier. However, the alpine vegetation belt of the Pyrenees is restricted by altitude (there is no more space available at higher altitudes), which would lead to dramatic losses in appropriate areas for different vegetation units. With the rise in altitude, the area of available habitat diminishes, the topography becomes more hostile (higher slopes) and the soil loses the power to sustain shrub and tree species (Benito et al. 2011). Therefore, as we expected and as our results show, the impact of climate change will mainly affect alpine vegetation units. Moreover, carbonated soils in the study area are limited to altitudes approximately below 2,700 m (ICC 1996); hence, calcareous vegetation units would also lack of suitable surfaces with the projected rise in altitude. As a consequence, we should be mindful of the risks calcareous alpine vegetation would face in the future.

This study confirmed a general trend found in studies based on species data conducted for Europe (Engler et al. 2011) and on regional scales (Dirnböck et al. 2003; Benito Garzón et al. 2008; Benito et al. 2011). As the climate becomes warmer and drier for the Oriental Pyrenees, alpine vegetation units can be expected to become relegated to summits, with their current range being taken over mainly by subalpine vegetation. Several works across the world have reported a force response in the altitudinal migration of plant species in New Zealand (Wardle and Coleman 1992) and in northern Europe (Kullman 2002), or in Alps, where resampling of vegetation in some areas has shown a significant increase in the number of shrub and herbaceous species in alpine ecosystems (Grabherr et al. 1994). More specifically, in the Mediterranean mountains, some studies have suggested that changes in temperature and precipitation would lead to a shift toward vegetation types currently found under drier conditions in Mediterranean mountains (Gritti et al. 2005). In a study performed in the Spanish Central Range, Sanz-Elorza et al. (2003) reported a replacement in high mountains grassland communities dominated by *Festuca aragonensis* by shrub patches of *Juniperus communis* and *Genista balansae* from lower altitudes. Furthermore, this altitudinal shift means that there will be increasingly restricted availability of potentially suitable areas for the analyzed alpine grassland units because, as mentioned above, the higher the altitude, the less the available surface area, being calcareous alpine grasslands more vulnerable due to the lack of carbonated soils above 2,700 m in the study area. This trend for alpine grasslands has also been observed in the Alps (Dirnböck et al. 2003), where similarly to the Oriental Pyrenees, alpine plant species show more limited availability of potentially suitable areas above the timberline over the years, so they will likely experience severe fragmentation and loss of suitable areas as a result of climate change. However, in alpine and subalpine environments, where the timberline is often maintained artificially at low altitudes by human activities, preservation of traditional land uses, such as pasturing, can decrease area losses for open vegetation that would become excluded through upward shifts of trees and reforestation of areas that are already suitable for forests under current climatic conditions (Theurillat and Guisan 2001; Dirnböck et al. 2003, 2011; Engler et al. 2011). Thus, a real challenge lies in the preservation of biodiversity of the mountain summits, since the species living there lack areas of expansion and will be subjected to great pressure, both by the degradation of the conditions appropriate to each species and by the arrival of new competitive species from lower altitudes (Benito et al. 2011).

A relatively recent study on the distribution of Iberian tree species is also noteworthy (Benito Garzón et al. 2008), in which the investigators used the *random forest* algorithm (RF) and projected losses in the size of the potential distribution area of *P. uncinata* on the Iberian Peninsula of approximately 92 % by the year 2080 under the conditions of the A2 scenario. This coincides with our results, which forecast a very similar percentage of 95 % of area lost (lost area based on the weighted average of each unit in group 42, *P. uncinata* forests) by 2080 under the same climate scenario. However, despite the loss of current area, these vegetation units are expected to be capable of altitudinal displacement and will therefore survive if they can colonize similar areas created by climate change. The extinction of some of the alpine and subalpine species would lead to a reduction in genetic diversity on the Iberian Peninsula, although it may be expected to survive in other European areas (Benito Garzón et al. 2008). A study performed regarding the future of the Alps also suggests that this species will survive at high altitudes (Theurillat and Guisan 2001).

A fine spatial resolution study in Europe (Engler et al. 2011) projects that an average of ~20 % of the plant species of European mountains areas could lose their entire suitable area by 2070–2100 under the A2 climate change scenario. This coincides with our results, which forecast a similar degree of threat to high mountain Pyrenees vegetation, with an average of 25 % of vegetation units projected to lose their entire suitable area by 2080 under this climate change scenario. Specifically, Engler et al. (2011) forecast that a maximum of 100 % of alpine species and 56 % of subalpine species will lose their entire suitable area in the Spanish Pyrenees by 2070–2100 under the A2 scenario. In contrast, our results forecast a much lower degree of threat to alpine and subalpine vegetation, with maximum levels of 50 and 0 % of alpine and subalpine units, respectively, projected to lose their entire suitable area by 2080 under this climate change scenario. The difference between these results is likely due to the different planimetric precision of the two studies, with the accuracy of CORINE vegetation units usually being much higher than that achieved in the case of species. Furthermore, we should note that this value of 100 % of alpine species that are projected to lose their entire suitable area by 2070–2100 in Engler et al. (2011) is based on only four species, so the actual average for all alpine species in the Pyrenees would be certainly lower, as found in this study. Nevertheless, our results coincide with the direction of the risks of predictions made by Engler et al. (2011) for the Spanish Pyrenees.

Hence, we note that models that predict future changes in the distribution of vegetation units can be as useful as those used in previous studies for species with the aim of obtaining better tools for policy planning related to biodiversity conservation. This study emphasizes that the investigated units could be potentially affected by climate change, and if we consider their high conservation value (as more than a half of the studied vegetation are of community interest under the 'Habitats' Directive 97/62/UE), we should consider implementing additional conservation efforts to ensure the future of these vegetation units. Moreover, these units shelter both endemic (e.g., *Dianthus vigoi*, *Festuca bordevei*, *Festuca yvesii*, *Armeria muelleri*) and threatened species (*Oxytropis lapponica*, *Pedicularis tuberose*, *Vaccinium vitis-idaea*), for which conservation either in situ or ex situ is essential.

Finally, we should note some intrinsic limitations of the methodology used in this study that should be considered when interpreting our results. The first of these limitations derives from the assumption that the climate forecast performed by the third IPCC working group for the next 70 years is correct. If the expected climatic patterns we used in this study do not match the future patterns exactly, such as a less pronounced increase in temperature occurring, the trends of altitudinal and range size changes predicted in this study may differ substantially. Another limitation to consider is related to the implementation of the limited dispersal scenario. For this, we used a statistical approach by applying a dispersal ability simulator of the vegetation units in the study area to their modelled future projections. However, the conditions that have led to the current range filling of the vegetation units might not exist in the future. Typically, the climate change scenario forecast changes in climate that are much faster than what happened in the past, and plants might not be able to migrate fast enough to keep up with the change. This means that the limited dispersal scenario used in this study probably overestimate the dispersal capacity of the vegetation units. The latter limitation to consider is that our models consider only the potential distribution of vegetation units as defined by bioclimatic envelopes (i.e., estimate the potential future distribution of vegetation based solely on environmental conditions) and therefore do not consider either competition phenomena or the ability of species to resist severe climatic conditions that are not lethal for their survival. Therefore, in light of these methodological limitations, the actual loss of area of occupancy of the studied vegetation units by 2080 could be considerably lower than predicted based on the results of this work. Nevertheless, our predictions provide important information about trends in the range sizes (occupation areas) of the studied vegetation formations.

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References

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour B (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Glob Change Biol 8:390–407

Beniston M (2000) Environmental change in mountains and uplands. Arnold/Hodder and Stoughton: Chapman and Hall Publishers, London

Beniston M, Fox DG, Adhikary S, Andressen R, Guisan A, Holten J, Innes J, Maitima J, Price M, Tessier L (1996) The impacts of climate change on mountain regions. Second assessment report of the intergovernmental panel on climate change (IPCC), Chapter 5. Cambridge University Press, Cambridge, pp 191–213

Benito Garzón M, Sánchez de Dios R, Saiz Ollero H (2008) Effects of climate change on the distribution of Iberian tree species. Appl Veg Sci 11:169–178

Benito B, Lorite J, Peñas J (2011) Simulating potential effects of climatic warming on altitudinal patterns of key species in mediterranean-alpine ecosystems. Clim Change 108:471–483

Bolliger J, Kienast F, Zimmermann NE (2000) Risks of global warming on montane and subalpine forest in Switzerland—a modeling study. Reg Environ Change 1:99–111

Botkin DB, Saxe H, Araujo MB et al (2007) Forecasting the effects of global warming on biodiversity. Bioscience 57:227–236

Braun-Blanquet J (1948) La vegetation alpine des Pyrérées Orientales. CSIC, Barcelona

Carreras J, Carrillo E, Ferré A, Ninot JM (2003) Mapa digital dels Habitats d'Andorra 1:25,000, [CD-Rom]. Centre de Biodiversitat, Institut d'Estudis Andorrans. Available from: http://www.iea.ad/

Carrillo E, Ninot JM (1992) Flora i Vegetació de les valls d'Espot i de Boí, 2. Arch Secc Cienc 99:1–350

Carson DJ (1999) Climate modelling: achievements and prospect. Q J R Meteorol Soc 125:1–27

Castro J, Zamora R, Hódar JA, Gómez JM, Gómez-Aparicio L (2004) Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. Restor Ecol 12(3): 352–358

Dirnböck T, Dullinger S, Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. J Biogeogr 30:401–417

Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob Change Biol 17:990–996

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Engler R, Randin CF, Vittoz P, Czáka T, Beniston M, Zimmermann NE, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography 32:34–45

Engler R, Randin CF, Thuiller W et al (2011) 21st century climate change threatens mountain flora unequally across Europe. Glob Change Biol 17:2330–2341. doi:10.1111/j.1365-2486.2010.02393.x

Erschbamer B (2001) Responses of some Austrian glacier foreland plants to experimentally changed microclimatic conditions. In:

Walther GR, Burga CA, Edwards PJ (eds) Fingerprints of climate change. Adapted behavior and shifting species range. Kluwer, New York, pp 263–279

ESRI (2009) ArcGIS 9.3. Environmental Systems Research Institute, Redlands, California, US

Ferrier S, Guisan A (2006) Spatial modelling of biodiversity at the community level. J Appl Ecol 43:393–404

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Fitzpatrick MC, Gove AD, Sanders NJ, Dunn RR (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the Banksia (Proteaceae) of Western Australia. Glob Change Biol 14:1–16

Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature 369:448

Gritti ES, Smith B, Sykes MT (2005) Vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. J Biogeogr 33:145–157

Guisan A, Rahbek C (2011) SESAM—a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. J Biogeogr 38:1433–1444

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (Roc) curve. Radiology 143:29–36

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773–785

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Glob Change Biol 12:2272–2281

Hijmans RJ, Cameron S, Parra J, Jones P, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Institut Cartogràfic de Catalunya (ICC) (1996) Mapa Geològic de Catalunya 1:250,000. Institut Cartogràfic de Catalunya, Departament de Política Territorial i Obres Públiques, Generalitat de Catalunya, Barcelona, Spain

Institut Cartogràfic de Catalunya (ICC) (2010) Base topogràfica de Catalunya 1:50,000. Institut Cartogràfic de Catalunya, Departament de Política Territorial i Obres Públicas, Generalitat de Catalunya. Barcelona, Spain

IPCC (2007) Climate change 2007: the physical science basis. In: Solomon S et al (eds) Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Jalas J, Suominen J (1972-1996) Atlas Florae Europaeae. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki, FI

Jiménez-Valverde A, Lobo JM (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. Acta Oecol 31:361–369

Körner C (2003) Alpine plant life, 2nd edn. Springer, Berlin

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. J Ecol 90(1):68–77

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393

Manel S, Williams HC, Ormeod SJ (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. J Appl Ecol 38:921–931

Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int J Climatol 25:693–712

Mitchell TD, Carter TR, Jones PD, Hulme M, New M (2004) A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 Scenarios (2001–2100). Tyndall Centre for Climate Change Res. [Working Paper 55], Norwich, UK

Nakicenovic N, Swart R (2000) Emission scenarios. Special report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol S 37:637–669

Pauli H, Gottfried M, Grabherr G (2001) High summits of the Alps in a changing climate. The oldest observation series on high mountain plant diversity in Europe. In: Walther GR, Burga CA, Edwards PJ (eds) Fingerprints of climate change. Adapted behaviour and shifting species range. Kluwer, New York, pp 139–149

Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. Glob Change Biol 13:147–156

Pausas JG, Carreras J, Ferré A, Font X (2003) Coarse-scale plant species richness in relation to environmental heterogeneity. J Veg Sci 14:661–668

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny Mountains (NE Spain). Glob Change Biol 9:131–140

Peterson AT, Papeş M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30:550–560

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–256

Phillips SJ, Dudik M, Elith J et al (2009) Sample selection bias and presence-only models of species distributions: implications for selection of background and pseudo-absences. Ecol Appl 19:181–197

Rosenzweig C, Karoly D, Vicarelli M et al (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357

Sanz-Elorza M, Dana ED, Gonzalez A (2003) Changes in the high mountain vegetation of the central Iberian Peninsula as a probable signo f global warming. Ann Bot 92:1–8

Shaw MR, Loik ME, Harte J (2000) Gas exchange and water relations of two Rocky Mountain shrub species exposed to a climate change manipulation. Plant Ecol 146:197–206

Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. Clim Change 50:77–109

Thomas CD, Cameron A, Green R et al (2004) Extinction risk from climate change. Nature 427:145–148

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. P Natl Acad Sci 102:8245–8250

Vigo J, Carreras J, Ferré A (2006) Cartografia dels hàbitats a Catalunya. Manual d'interpretació. Generalitat de Catalunya, Departament de Medi Ambient i Habitatge, Barcelona. Available from: http://www.ub.edu/geoveg/en/semhaveg.php

Viviroli D, Weingartner R (2004) Hydrological significance of mountains: from regional to global scale. Hydrological earth systems. Science 8:1016–1029

Walther GR, Post E, Convey P et al (2002) Ecological responses to recent climate change. Nature 416:389–395

Walther GR, Beissner S, Burga CA (2005) Trends in the upward shift of alpine plants. J Veg Sci 16:541–548

Wardle P, Coleman MC (1992) Evidence for rising upper limits of 4 native New-Zealand forest trees. New Zeal J Bot 30(3): 303–314