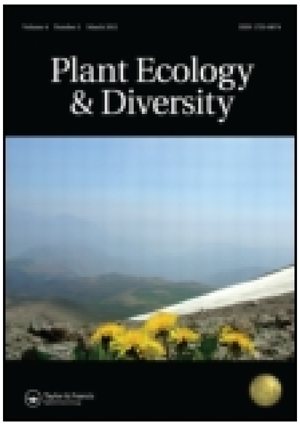

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Status and conservation of Silene section Cordifolia in the Iberian Peninsula: a menaced group under global environmental change

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Status and conservation of *Silene* section *Cordifolia* in the Iberian Peninsula: a menaced group under global environmental change

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Background: Detailed knowledge of a species' autecology as well as information on the availability of suitable habitats and the impacts of climate change on the species and its habitat are requirements for adequate conservation planning. For this purpose, species distribution modelling has been suggested as an effective tool to assess the potential geographic distributions of species under different climate scenarios.
Aims: The aim of this study was to generate suitability maps and predictive maps based on scenarios of climate change to identify areas with the most value for conservation for the western Iberian endemics *Silene acutifolia*, *S. foetida* subsp. *foetida* and *S. foetida* subsp. *gayana*.
Methods: Maxent software was used to model and predict the distribution of the species based on environmental variables under climate change scenarios.
Results: Our analysis indicated that the models performed well, predicting with high accuracy the current distributions of the species. Under two scenarios of increasing CO_2, the species were predicted to be susceptible to a major reduction of suitable habitat; both *S. foetida* subspecies were shown to be at risk of extinction.
Conclusions: Our findings suggest that the inclusion of *S. foetida* in national conservation and long-term monitoring programmes must be considered.

Keywords: climate change; endemic species; Maxent; species distribution modelling; suitable habitat prediction

Introduction

Evidence of climatic change altering the distribution of many species is accumulating (Parmesan et al. 1999; Hickling et al. 2005) and more change in the future is inevitable (Maclean et al. 2008; Anderson et al. 2009). Rapid climate change leaves a clear fingerprint on global biodiversity (Gregory et al. 2009) and locally is a major challenge for conservationists (Peterson et al. 2002; Thomas et al. 2004). Adequate conservation not only requires detailed knowledge of a species, of its natural history and biology, but also information on the availability of suitable habitats at present and under future climate scenarios (Hu et al. 2010), and the impacts of climate change on the species and on habitat suitability (Araújo et al. 2004; Hole et al. 2009). Such data are invaluable for conservation planning and the selection of protected areas (Papes and Gaubert 2007). Therefore, an increasing concern over the future of biodiversity has led scientists to develop tools to model current species distribution and their response to global environmental change. For this purpose, species distribution modelling (i.e. niche or habitat potential distribution) has been suggested as an effective tool to assess the potential geographic distributions of species (Guisan and Thuiller 2005; Elith et al. 2006; Pearson et al. 2007; Hu and Jiang 2010). Rapid progress in this area of prediction has been made and tools are now available to assess the potential impacts of climate change on the distribution of climate-determined habitats (Peterson et al. 2002; Hijmans and Graham 2006). A complete comparison of current and future predicted distributions of species enables conservationists to develop conservation and project plans with a view of current and future needs (Araújo and Rahbek 2006).

A variety of species distribution modelling methods are available to predict potential suitable habitat distribution for a species (Guisan and Zimmermann 2000; Elith et al. 2006; Guisan et al. 2007a,b; Wisz et al. 2008); however, comparatively few predictive models have been used for rare and endangered plant species alone (Engler et al. 2004; Guisan and Thuiller 2005), and very few examples of studies using small sample sizes are published (Pearson et al. 2007; Thorn et al. 2009). Most species distribution modelling methods are sensitive to sample size (Wisz et al. 2008), and may not accurately predict habitat distribution patterns for threatened and endangered species. Factors driving the distribution and abundance of organisms often act at different spatial scales (Wiens 1989, Wiens 2002; Pearson et al. 2004; Guisan and Thuiller 2005; Guisan et al. 2007a),

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making modelling species distribution a challenging procedure (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith and Leathwick 2007; Murphy and Lovett-Doust 2007; Randin et al. 2009).

Maxent is a modelling software that uses the maximum entropy distribution probability function, i.e., the most unconstrained one (Jaynes 1957), to predict the location of species based on environmental variables. Only presence data is required to create a model that assigns each grid cell a species presence probability, based on environmental suitability (Phillips et al. 2006; Phillips and Dudik 2008).

The present study focuses on *Silene* sect. *Cordifolia*, which includes the Iberian endemics *Silene acutifolia* Link., *S. foetida* L. subsp. *foetida* and *S. foetida* L. subsp. *gayana* Talavera. These taxa occur exclusively in rocky habitats; *S. acutifolia* appears in fissures of granitic rocks while *S. foetida* subsp. *foetida* and *S. foetida* subsp. *gayana* appear on shallow soils, screes and rocky slopes (Talavera 1990).

Silene sect. *Cordifolia* is confined to the north-western part of the Iberian Peninsula. Several glacial events affected this area during the Pleistocene (Lemartinel 2004) and profound future climatic changes resulting from anthropogenic activities are forecast (Solomon et al. 2007).

The objectives of the study were to (1) generate suitability maps of the current distribution for endemic species with reduced distribution, using herbaria occurrence records; (2) identify the environmental factors associated with these species habitat distribution; (3) generate predictive maps of future distribution based on scenarios of climate change, and identify the areas with the highest value to conservation.

Methods

Occurrence data

Information on the occurrence of the species was collected from 341 vouchers from the following Iberian herbaria (abbreviations according to Index Herbariorum; Thiers 2010): AVE, BRESA, COI, EAN, HVR, LISI, LISU and PO in Portugal, and GDA, LEB, MA, MGC, SALA, SANT, SEV and VAL in Spain. To map the distribution of these taxa, occurrences were geographically referenced using a grid with resolution of 1 km^2 according to the pixel resolution of the environmental variables used, as recommended by Gutiérrez and Pons (2006) for regional scales. Less precise occurrence data ($>$ 1 km^2) were not used to prevent errors related to topographic characteristics, although location errors up to 5 km appear to have no impact on model performance (Graham et al. 2008).

Study area

The distribution of target species extends from central Portugal to Asturias in Spain (Figure 1). The region is geologically complex (Miller et al. 2009), with several lithological substrates and an altitudinal range from sea level to 2648 m above sea level in Asturias. The south-eastern region of the study area has a Mediterranean pluvio-seasonal oceanic or temperate oceanic bioclimate (Costa et al. 1999; Rivas-Martínez et al. 2004; Capelo et al. 2007), where oromediterranean vegetation shows some affinities with that of other southern Mediterranean mountains (Garcia et al. 1998). The northern part of the distribution area is characterised by a temperate climate and by a more mesophilous vegetation (Sobrino et al. 2004).

Silene acutifolia is found mainly on granite, and *S. foetida* on schists and quartzite. *S. acutifolia* lives in supratemperate, orotemperate and submediterranean chasmophytic communities (the Saxifragion willkommianae alliance of Rivas-Martínez 1974). *Saxifraga foetida* occurs on stony slopes (communities of the alliance Linario–Senecionion carpetani, Rivas-Martínez 1974). Both alliances are endemic to the north-western quadrant of the Iberian Peninsula (Rivas-Martínez et al. 2002). Other rare and endemic taxa found in these communities include *Festuca henriquesii* Hack., *Festuca summilusitana* Franco & Rocha Afonso, *Centaurea micrantha* Hoffmanns. & Link subsp. *herminii* (Rouy) Dostal, *Allium ericetosum* Thore subsp. *palentinum* (Losa & Monts.) Laínz, *Armeria humilis* (Link) Schult. subsp. *odorata* (Samp.) P. Silva, *Armeria humilis* (Link) Schult. subsp. *humilis*, *Centaurea limbata* Hoffmanns et Link. subsp. *geresensis* (Arènes) Franco, *Phalacrocarpum oppositifolium* (Brot.) Willk., *Murbeckiella boryi* (Boiss.) Rothm., *Rumex suffruticosus* J. Gay ex Willk. (Ortíz and Rodríguez-Oubiña 1993; Honrado 2003).

Environmental data

Twenty-three environmental variables (Table S1, see the supplementary material which is available via the multimedia link on the online article webpage) were considered initially as potential predictors for *Silene* sect. *Cordifolia* current habitat distribution, based on their biological relevance to plant species distributions and on several other habitat modelling studies (Kumar et al. 2006; Guisan et al. 2007a,b; Pearson et al. 2007; Murienne et al. 2009; Kumar and Stohlgren 2009). The 23 variables were chosen as being biologically most meaningful to relate to eco-physiological tolerances of a species (Hijmans and Graham 2006; Murienne et al. 2009), and were obtained from WorldClim (http://www.worldclim.org; Hijmans et al. 2005).

Collinearity of variables can lead to statistical bias and model over-prediction. In order to avoid such problems, variables were subjected to cross-correlations (Pearson correlation coefficient, r), based on the values for each one of the 341 species occurrence records. A Principal Component Analysis (PCA) was carried out, based on the correlation matrix, in order to detect groups of variables (to obtain the underlying relationships of variables, Hair et al. 1995). For further analysis, variables within the groups of variables obtained by PCA with the highest correlation values per correlation group were selected (Iman and Conover 1989) to improve the statistical robustness of the results.

For *S. acutifolia,* temperature seasonality (standard deviation ×100), annual temperature range, mean temperature of wettest quarter and precipitation seasonality

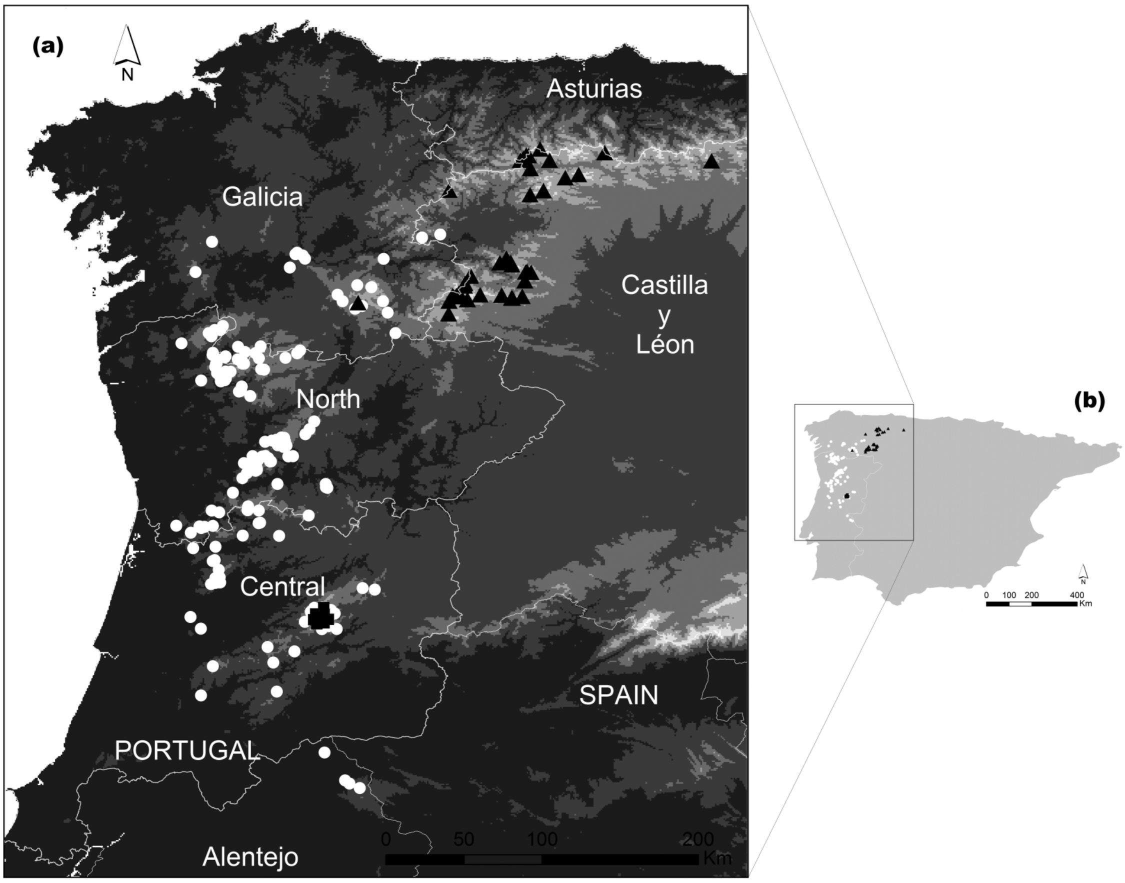

Figure 1. The distribution range of *Silene* sect. *Cordifolia* in northern Spain and northern and central Portugal (a), Iberian Peninsula (b). Black square, *Silene foetida* subsp. *foetida*; black triangle, *S. foetida* subsp. *gayana*; white circle, *S. acutifolia* in northern Spain and northern and central Portugal (a). In (a) background gradient indicates elevation; lighter colours correspond to areas with higher altitude.

(coefficient of variation) were chosen. For *S. foetida* subsp. *foetida* elevation, annual precipitation and precipitation of wettest month, and for *S. foetida* subsp. *gayana* elevation, mean annual temperature, mean diurnal range, mean temperature of coldest quarter and precipitation of coldest quarter.

The climate predictors were derived from a general circulation model (CCCMA: CGCM2) for the years 2020, 2050 and 2080 under IPCC emission scenarios (SRES; A2a and B2a) for predicting future potential habitats (http://gisweb.ciat.cgiar.org/GCMPage; Ramirez and Jarvis 2008). A2a and B2a represent two scenarios with different greenhouse gas emissions. A2a describes a highly heterogeneous future world with regionally oriented economies. The B2a scenario is also regionally oriented but with a general evolution towards environmental protection. Compared to A2a, B2a has a lower rate of global warming and therefore changes in temperature and precipitation are less intense (http://forest.jrc.ec.europa.eu/climate-change/future-trends).

Modelling of species distribution

Maxent estimates the probability distribution of a species occurrence based on environmental constraints (Phillips et al. 2006). It requires only species presence data and environmental variables in GIS layers for the study area. We used Maxent v. 3.3, to estimate the probability of potential suitable habitat for species occurrence ranging from 0 to 1, where 0 is the lowest and 1 the highest probability.

Testing or validating the fit or accuracy of the modelling approach, as well as determining the probability that locations which indicated presence of a species was ranked higher than a random background probability, were made through receiver-operating characteristic (ROC) plots (Fielding and Bell 1997) and area under curve (AUC) approaches (Phillips et al. 2006). Locations with a random background probability served as pseudo-absences for all analysis in Maxent (Phillips et al. 2004; Phillips et al. 2006).

Ideally, test data would be collected independently from the data used to calibrate the model; however, in practice it may not be possible to obtain independent test data and it is therefore common to partition the available data into calibration and test datasets. Several strategies are available for partitioning data (Pearson 2007): by using independent data from different regions (Beerling et al. 1995); data at different spatial resolution (Araújo et al. 2005b; Pearson et al. 2004); and data from surveys conducted by other researchers (Elith et al. 2006). Here we followed Araújo et al. (2005a), and used data from different time periods to calibrate the model. These data were obtained from recent field surveys by the authors.

One of the objectives of the study was to understand how each of the chosen environmental variables influenced the presence of the modelled species. The method followed for assessing variable importance was the jack-knife approach. Maxent's jack-knife test of variable importance can be used to evaluate the relative strengths of each predictor variable (Yost et al. 2008). The training gain is calculated for each variable alone as well as the drop in training gain when the variable is omitted from the full model (Phillips et al. 2006).

For all models the following parameters were used: 10 repetitions with cross-validation, standard regularisation multiplier (affects how focused or closely-fitted the output distribution is) and 500 iterations (for further details on these parameters see Phillips 2010). The obtained output (in ASCII format) was input into ArcGIS software version 9.2 (ESRI, Redlands, California, USA) as floating-point grids (Peterson et al. 2007) and occurrence probability of the species at each site was mapped.

Results

Potential distribution area

Model outputs clearly identified central and north Portugal and Galicia in Spain as containing highly suitable habitats for *S. acutifolia*. Of the three studied taxa, this is the most widespread taxon, and areas with high probabilities of suitable habitat were identified (Figure 2a). Suitable habitat for *S. foetida* subsp. *foetida* was predicted only in the Serra da Estrela (Figure 2b) with maximum probabilities of 0.64. This clearly showed the specificity of the taxon to the area, from where all known records originate. The model for *S. foetida* subsp. *gayana* also identified regions with high probabilities of suitable habitat in northern Spain (Galicia, Asturias and Castilla y Leon) (Figure 2c).

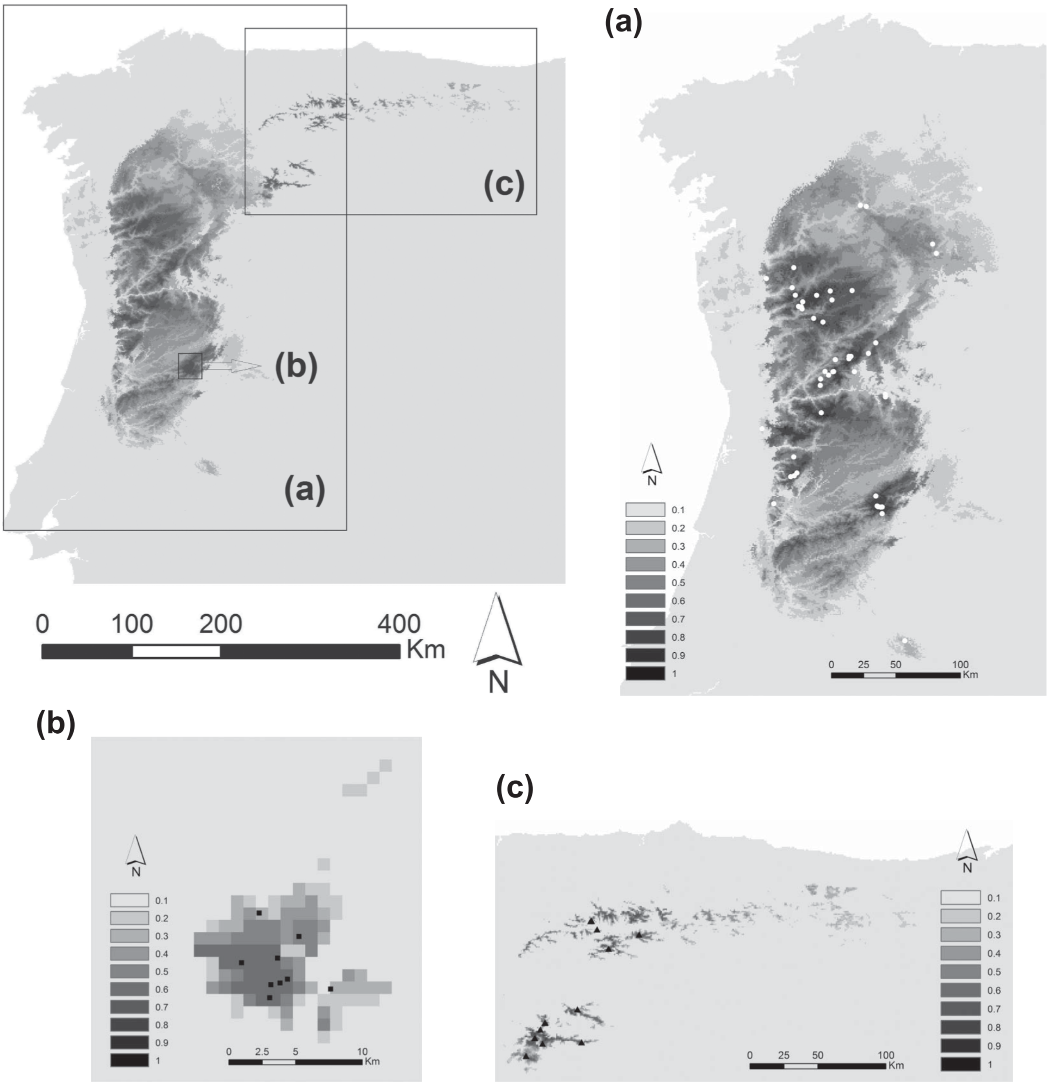

Figure 2. Current predicted suitable habitat maps for (a) *Silene acutifolia* (white circles indicate occurrence points used for model evaluation); (b) *Silene foetida* subsp. *foetida* (black squares indicate occurrence points used for model evaluation); (c) *Silene foetida* subsp. *gayana* (black triangles indicate occurrence points used for model evaluation).

The ROC analysis indicated that the model performed well with high predictive accuracy compared to the value expected (0.5) from a random prediction (see Figure S1 of the supplementary material). It was supported by AUC values of 0.985 for *S. acutifolia*, 0.999 for *S. foetida* subsp. *foetida* and 0.997 for *S. foetida* subsp. *gayana*.

Environmental analysis

Jack-knife analysis indicated that mean temperature of the wettest quarter for *S. acutifolia*, annual precipitation and mean annual temperature for *S. foetida* subsp. *foetida* and *S. foetida* subsp. *gayana* respectively, contributed the most to the model when variables were used alone (Figure S2 of the supplementary material). Nevertheless, and taking into consideration the small number of variables used in model development, all of them showed a high value of importance. The amplitude values of the most important variables for each taxon are shown in Table 1.

Potential effects of climate change

Our results indicated potential changes in the distribution range i.e., in the extent of the area of suitable habitat, and in the quality of suitable habitat (Table 2) for all of the studied taxa under future climate change scenarios. Although greenhouse gas emissions from the two scenarios are predicted to affect global climate change in different ways (http://forest.jrc.ec.europa.eu/climate-change/future-trends), the area of suitable habitat was projected to have a similar geographic displacement and reduction with both scenarios. Disappearance of suitable habitat was predicted in some cases.

For A2a scenario, a geographic displacement towards the north was predicted for *S. acutifolia* (Figure 3a), together with a loss of suitable habitat and a reduction in its area by up to 76% by 2080. *S. foetida* subsp. *foetida* appeared to be the most affected by climate change. Projections pointed to more than 90% of suitable habitat loss by 2050 and total extinction by 2080 (Figure 3b). *S. foetida* subsp. *gayana* was predicted to have a continuous decrease of suitable habitat, declining to 45% of current values by 2080 (Figure 3c) and a reduction in its area occupation of up to 93%.

Predictions under the B2a scenario were similar to those under A2a, differing mainly in the extent of suitable habitat area loss (Table 2). For *S. acutifolia* (Figure 4a) a decrease of habitat suitability to maximum values of 70% and 68% by 2050 and 2080 respectively, was observed. It was predicted to have up to 57% reduction in its suitable habitat

Table 1. The ranges of values per taxon of the most important environmental variables in model development. Elev, elevation; AMT, annual mean temperature; MDR, mean diurnal range; TS, temperature seasonality; TAR, temperature annual range; MTWtQ, mean temperature wettest quarter; MTCQ, mean temperature coldest quarter; AP, annual precipitation; PWtM, precipitation wettest month; PS, precipitation seasonality; PCQ, precipitation coldest quarter.

	Silene acutifolia		*Silene foetida* subsp. *foetida*		*Silene foetida* subsp. *gayana*	
	Min	Max	Min	Max	Min	Max
Elev (m)	60	1915	1693	1960	1580	2270
AMT (°C)	6.2	16.4	5.9	7.3	3.0	7.0
MDR (°C)	6.9	10.9	7.1	7.3	8.8	10.2
TS	4131	5655	5267	5345	5082	5623
TAR (°C)	20.8	26.5	21.9	22.3	23.8	26.4
MTWtQ (°C)	3.0	10.3	1.0	1.5	−2.2	3.3
MTCQ (°C)	3.0	10.3	1.0	1.5	−2.9	6,0
AP (mm)	769	1790	1739	1798	1003	1437
PWtM (mm)	104	271	262	267	121	184
PS	40	58	53	55	24	41
PCQ (mm)	277	717	703	716	285	527

Table 2. Probability values of habitat suitability (PHS) and remaining percentage of current area (RPCA; %) for *Silene* sect. *Cordifolia* using two scenarios (A2a and B2a) for four-time slices (2000, 2020, 2050 and 2080).

	Silene acutifolia				*Silene foetida* subsp. *foetida*				*Silene foetida* subsp. *gayana*			
	0.81 (PHS)				0.64 (PHS)				0.81 (PHS)			
Year\Species	A2a		B2a		A2a		B2a		A2a		B2a	
2000	PHS	RPCA	PHS	RPCA	PHS	RPCA	PHS	RPCA	PHS	RPCA	PHS	RPCA
2020	0.76	83	0.77	84	0.25	18	0.25	62	0.80	45	0.96	94
2050	0.70	62	0.70	63	0.24	70	0.16	22	0.67	25	0.83	80
2080	0.58	24	0.68	43	0	0	0.14	15	0.45	30	0.73	29

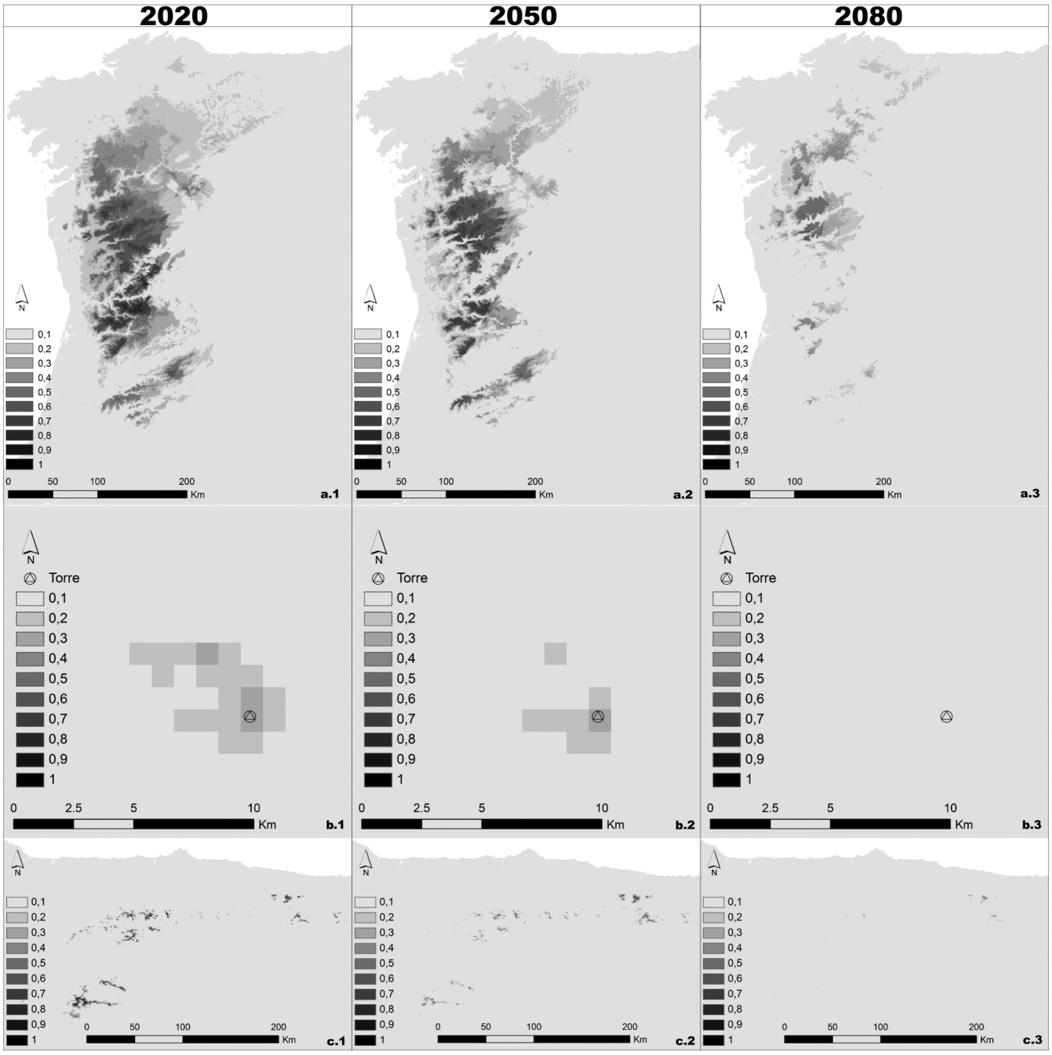

Figure 3. Predicted suitable habitat for (a) *Silene acutifolia*; (b) *Silene foetida* subsp. *foetida*; (c) *Silene foetida* subsp. *gayana*; obtained with an ensemble-forecast approach across the general circulation models CCCMA for three time slices (2020 (1), 2050 (2) and 2080 (3)) and one storyline (A2a).

area by 2080 (Figure 4b). *S. foetida* subsp. *foetida* was projected to have a suitable habitat maximum value of 30% and a reduction in its area by 85% (Figure 4b). *S. foetida* subsp. *gayana* was also predicted to have a continuous decrease of suitable habitat area with 92% loss by 2080 (Figure 4c) but without loss of habitat suitability. In this case it is important to point out the increase of habitat suitability by 2020 and 2050, and a minor decrease in 2080 (Table 2).

Discussion

Model evaluation

Species distribution models are now widely used in ecology, biogeography and conservation mostly to predict species distributions by combining known occurrence records with a set of environmental variables (Guisan and Zimmermann 2000; Pearson 2007). Nonetheless, it is crucial to understand the concepts and applications of distribution models to ensure the appropriate interpretation of their predictions (Guisan and Thuiller 2005; Soberon and Peterson 2005; Elith and Graham 2009). One important application of species distribution models refers to their ability to predict the potential areas of occurrence for rare or threatened species, under current and future environmental conditions (Pearson et al. 2007; Kumar and Stohlgren 2009; Thorn et al. 2009).

In our study of Iberian *Silene* taxa, the complete overlap of the predicted current suitable habitat with the presently known populations (used for testing) for each of the three *Silene* taxa indicated that the models had an excellent fit to the data. In our study the models performed well, with high predictive accuracy and AUC values ranging from 0.985 to 0.997, sufficiently accurate for a useful contribution to conservation planning applications (Pearce and Ferrier 2000). Other areas with highly suitable habitat were also identified. These results are relevant because reliable spatial predictions are essential for species of great conservation interest (Pearce and Ferrier 2000; Guisan et al. 2005).

The maps for the potential suitable areas mostly correspond to the current knowledge about the distribution for *S. acutifolia* and *S. foetida* subsp. *foetida*. For *S. foetida* subsp. *gayana* some areas of potential suitable habitats are

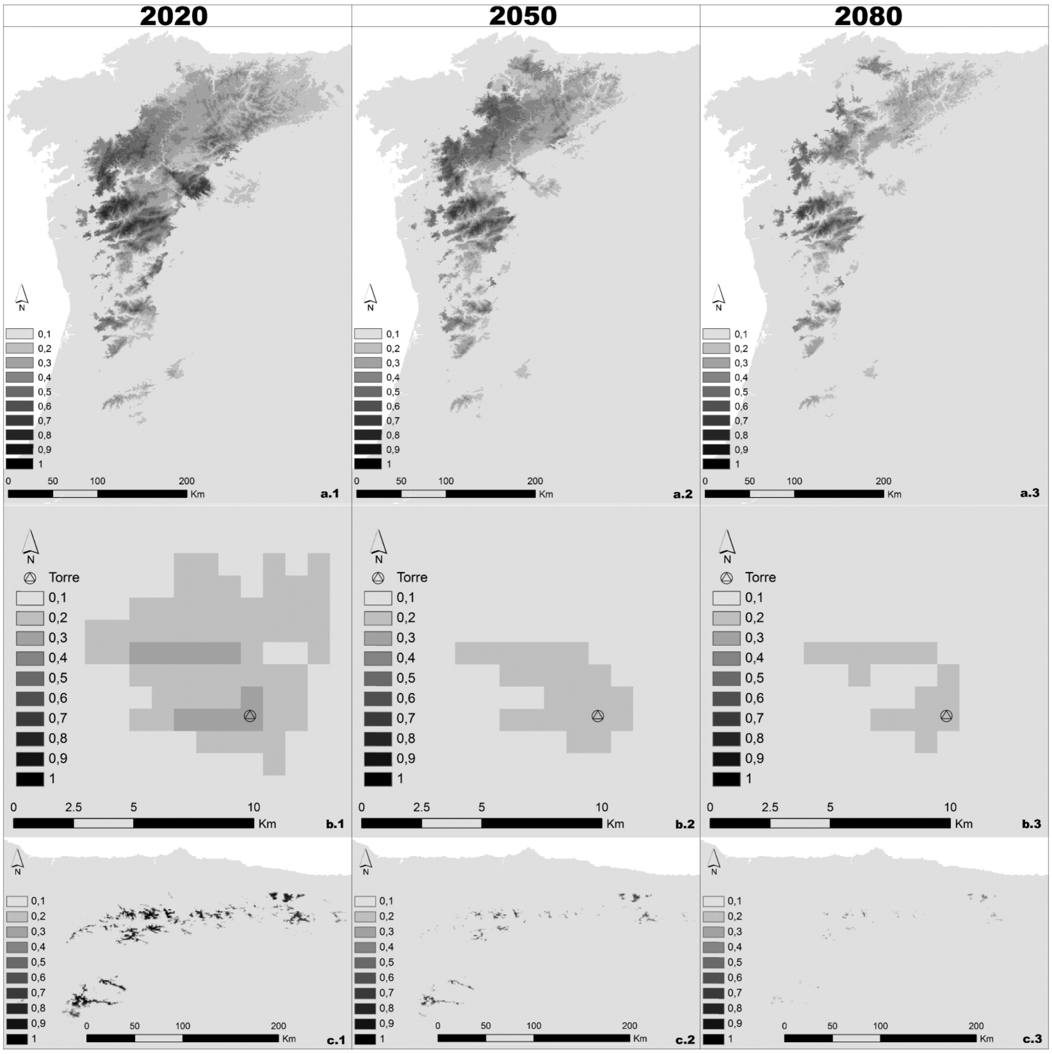

Figure 4. Predicted suitable habitat for (a) *Silene acutifolia*; (b) *Silene foetida* subsp. *foetida*; (c) *Silene foetida* subsp. *gayana*; obtained by an ensemble-forecast approach across the general circulation models CCCMA for three time slices (2020 (1), 2050 (2) and 2080 (3)) and one storyline (B2a).

in localities with difficult or no access at all. This is common in models where suitable habitats are predicted based on climate alone (Ledig et al. 2010). Many other factors may restrict actual species occurrence, for example, substrate, interactions with other species, snow cover or restrictions to seed dispersal (Pearson and Dawson 2003; Ledig et al. 2010). Therefore field surveys would be required to determine the actual presence of *S. foetida* subsp. *gayana* in those locations. According to Engler et al. (2004) it would be expected that for both *S. foetida* subspecies the predicted areas of distribution were very close to the real distribution because many rare and threatened species tend to occupy most of their potential habitats, which have usually been drastically reduced by habitat or environmental limitations.

Determining factors that affect species distributions and habitat selection and identifying which variables have the greatest influence on the model and on species occurrence is fundamental (Baldwin 2009). Vicente et al. (2011) have proposed that environmental variables can be divided into two types: climate variables and meso-scale terrain morphology usually act on a regional scale; whilst soil type, landscape structure and habitat conditions act on a local scale. Austin and van Niel (2011) stressed the importance of variable selection and pixel resolution for modelling. In our study, a regional approach was used in line with studies by Randin et al. (2009), Ledig et al. (2010) or Austin and van Niel (2011), yet there are limitations to using only terrain and climatic variables and this should be taken into consideration. The quality of our distribution models is related to the restricted distribution of the taxa studied, as well as by their exclusive occurrence in rocky habitats.

Our results show differentiation for the taxa analysed with the environmental variables used. The altitudinal values indicate a highly variable range for *S. acutifolia*, in contrast with the two subspecies of *S. foetida*, both with ranges at elevations higher than 1500 m. High or moderately high precipitation throughout the year is important for all three taxa, and the distribution of precipitation over the year is important for *S. acutifolia* and *S. foetida* subsp.

foetida. In contrast, *S. foetida* subsp. *gayana* is associated with lower precipitation and temperature values during the colder months. Opposite behaviour was observed for *S. foetida* subsp. *foetida*, with a small range of temperatures through the year. The wider range of temperatures observed for *S. acutifolia* is explained by a wider geographic and altitudinal range i.e., a more heterogeneous environmental envelope.

Potential effects of climate change

Applying the IPCC SRES scenarios indicated a progressive and severe reduction of climatically suitable habitats in the present ranges of all studied taxa. In line with the findings of Pauli et al. (2003), which state that endemics with a narrow altitudinal distribution area close to summits are the most susceptible to extinction, for *S. foetida* subsp. *foetida* the loss of all its suitable habitats was predicted. For *S. foetida* subsp. *gayana* the most important result was the reduction in the area of suitable habitat. For this taxon, in the B2a scenario, it was forecast that suitable habitat values would increase but its area would nevertheless decrease. As mentioned before, *S. foetida* subsp. *gayana* is primarily temperature-driven, and because the most important variables in model development are temperature-related (Figure S2), with the increase of temperatures in the scenarios analysed, its suitable habitat will move up to higher ranges, therefore decreasing its area of potential habitat. These results are in line with the results of several other studies, such as those of Araújo et al. (2005a), Pauli et al. (1996), Pauli et al. (2003), van der Putten et al. (2010), Bässler et al. (2010) and Gottfried et al. (2012). The main area of refuge for *S. foetida* subsp. *gayana* by 2080 appears to be in the north-eastern mountains of its current range as, in possible future trends, plant species in general would find their current climate envelopes further north-east (Bakkenes et al. 2002; Wiens et al. 2009).

The forecasts for *S. acutifolia* showed a displacement of its suitable area in the north along with a clear decrease and fragmentation of its occurrence area, and also a decrease in the quality of the habitat, following the results of Ozinga et al. (2007). Nevertheless, predicted suitable habitats in 2020, 2050 or 2080 based on current climate niches for *S. acutifolia* seem to share areas from its present distribution, and therefore this spatio–temporal connectivity could allow a reasonable expectation of natural colonisation (Bèlisle 2005).

In the application of our model, we stress that projections of suitable climate represent the future distribution of climates bounding the contemporary realised climate niche. Although additional niche space may become available in future climate changes, one can conclude with little uncertainty that future analogues to the realised niche of today will indeed be suitable for populations of the future (Ledig et al. 2010).

The main scenarios predict, at global level, important climatic alterations for the Iberian Peninsula during the twenty-first century (Hulme and Sheard 1999), and the used scenarios demonstrated conspicuous alterations of the modelled distribution for all three taxa. Current cold-limited bioclimatic belts in Mediterranean mountains are expected to decrease dramatically by becoming warmer (Metzger et al. 2008; Nagy et al. 2010), which would have major implications for mountain plant species, particularly threatening endemic species (Pauli et al. 2003). Strong changes in temperature/precipitation regimes have been predicted for this area (Rodriguez-Puebla et al. 1998; OrtizBévia et al. 2011) and the disappearance of the habitat occupied by these taxa (scenarios A2a and B2a) is therefore expected. In the case of mountain flora, progressive competition (and eventually replacement) by more thermophilous taxa is predicted as a probable change (Theurillat and Guisan 2001; Beniston 2003; Gottfried et al. 2012) as a direct result of alterations in the precipitation regime, and a high degree of complexity of associated variables (Beniston et al. 1997). The study area represents the western-most occurrence of the taxa studied and the western-most extreme of the Eurosiberian bioclimatic domain (Capelo et al. 2007; Rivas-Martínez 1985). These factors could account for the predicted decrease in potential and occupied areas by the three *Silene* taxa.

Conservation and management implications

Guisan et al. (2005) and others have stressed the importance for nature conservation of modelling species distributions to identify factors that determine current range limits, to predict potential ranges of species, and to forecast future range shifts resulting from climate change. Our results illustrate some important considerations for conservation of the three *Silene* taxa. Firstly, the disappearance of suitable habitat, as in *S. foetida* subsp. *foetida*, may thwart conservation efforts. Secondly, suitable habitats under current IPCC global warming scenarios will move northward only for *S. acutifolia*. Neither *S. foetida* subspecies, due to their mountain range delimitation, can expect similar displacement. Thirdly, a species is an evolving unit and it may be necessary to consider intraspecific genetic differences. Not all individuals of a species will necessarily respond in the same way to changes in the environment (Ledig et al. 2010).

The predictions of range loss do not take into account the potential for adaptation (Skelly et al. 2007). Species also respond to climate change by dispersal to, and colonisation of, new suitable habitats. For most species, lack of information makes it difficult to predict colonisation responses (Neilson et al. 2005). Fragmentation of habitat and the subsequent geographic isolation of populations would invoke the biogeographic island effect (Kohn and Walsh 1994), particularly in the case of *S. acutifolia* and *S. foetida* subsp. *gayana,* and raise several questions related to genetic drift. The combination of ecogenetic (natural selection for current ecological conditions) and phylogenetic (historical events, including the effects of genetic drift and selectively neutral mutations) processes (Thorpe et al. 1994) can be envisaged: (1) current and future ecological barriers isolating populations of *S. foetida* subsp.

gayana and (2) a future genetic drift involving the development of several isolated populations of *S. acutifolia* as its distribution area becomes fragmented. In contrast, populations of *S. foetida* subsp. *foetida* occur concentrated in a narrow altitude range and therefore issues related to genetic diversity for this taxon are related essentially to population reduction as a consequence of habitat loss.

Although these endemic taxa are not considered threatened at the moment, based on our results, conservation measures must be assured especially for *S. foetida*. As the changes predicted for the *Silene* taxa are expected to have a similar effect on their companion species (Sanz-Elorza et al. 2003), which are also rare and have a narrow distribution ranges, such measures should naturally be applied to the species growing in association with *S. foetida*.

We believe that *S. foetida* subspecies occur at microsites. Microsites are limited by lithology and soils within the climatically suitable areas for *S. foetida* (Ladero et al. 1999; Talavera 1990), such as those high up the Serra da Estrela in Portugal or in the mountains of northern Spain. Such microsites are much narrower than the habitat predicted because, in the case of both *S. foetida* subspecies, the climate model is not yet capable of capturing microsite variations. Yet, it is also true that species do not occur in all places ideally suited to them i.e., a portion of the errors of models are due to correctly predicting niche space that is, by chance, not occupied (Ledig et al. 2010). Future work with a more detailed spatial resolution and the use of other local variables for both *S. foetida* subspecies would therefore be important when planning practical on-site conservation measures.

In conclusion, based on the results of our habitat modelling and on knowledge of the ecology of the taxa, we suggest the inclusion of both subspecies of *S. foetida* in national conservation and long-term monitoring programmes. On-site conservation measures, such as limiting access or preventing habitat alterations by infrastructure development or energy generation projects should be considered. Off-site conservation methods, such as seed banking, are another important measure to be decided on by conservation decision makers to preserve the taxa.

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