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Habitat-partitioning improves regional distribution models in multi-habitat species: a case study with the European bilberry

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Abstract

Modelling the spatial distribution of multi-habitat species is challenging since they show multi-dimensional environmental responses that may vary sharply through habitats. Hence, for these species, the achievement of realistic models useful in conservation planning may depend on the appropriate consideration of habitat information in model calibration. We aimed to evaluate the role of different types of habitat predictors, along with habitat-partitioning, to improve model inference, detect non-stationary responses across habitats and simulate the impact of sampling bias on spatial predictions. As a case study, we modelled the occurrence of the multi-habitat plant species bilberry (*Vaccinium myrtillus*) in the Cantabrian Mountains (NW Spain), where it represents a basic trophic resource for threatened brown bear and capercaillie. We used MaxEnt to compare a baseline model approach calibrated with topo-climatic variables against three alternative approaches using explicit habitat information based on vegetation maps and remote sensing data. For each approach, we ran non-partitioned (all habitats together) and habitat-partitioned models (one per habitat) and evaluated model performance, overfitting and extrapolation. The highest performance was for habitat-partitioned models including habitat predictors. The lowest overfitting was for the baseline non-partitioned model, at the cost of achieving the highest predicted fractional area. The extrapolation success of habitat-partitioned models was low, with the highest performance for the baseline approach. Our results highlight that multi-habitat species responses are non-stationary across habitats, with habitat-biased data resulting in weak spatial predictions. When modelling the distribution of multi-habitat species at regional scale, we recommend using habitat-partitioned models including habitat predictors, either vegetation maps or remote sensing data, to improve the realism of spatial outputs and its applicability in regional conservation planning.

Key-words. Habitat maps; stationary responses; truncated responses; *Vaccinium myrtillus*; vegetation predictive models.

Introduction

Species distribution modelling (SDM) is a correlative approach that allows mapping species distributions on the basis of environmental features (Elith and Leathwick 2009). Nowadays, SDM is a well-established method for designing conservation strategies and management actions (Morán-Ordóñez et al. 2011; Carlson et al. 2013). However, the achievement of accurate model predictions at high spatial resolution is still a challenge for practical applications. It is recognized that the reliability of SDM predictions depends significantly on the characteristics of the input data used for model calibration (Guisan et al. 2013), which includes both the dependent (i.e. occurrence data quantity, quality and distribution; Hernandez et al. 2006; Kramer-Schadt et al. 2013; Suárez-Seoane et al. 2017, 2018) and the independent (i.e. environmental predictors' nature, source and scale; Austin 2002; Synes and Osborne 2011) variables. Other interacting factors that may influence critically the accuracy of model outputs are the ecological characteristics of the target species. In this sense, different authors have demonstrated that species with broad ecological requirements can be modelled less accurately than species with restricted requirements, independently of the SDM method (Brotons et al. 2004; Chefaoui et al. 2011; Morán-Ordóñez et al. 2012).

Particularly challenging is the modelling of multi-habitat species that exploit heterogeneous landscape mosaics, as thriving in different habitats may be related to ecological divergence across the species´ range (Brambilla and Saporetti 2014; Frans et al. 2017; Ikeda et al. 2017; Maiorano et al. 2019). A main concern affecting the achievement of accurate predictions for multi-habitat species is habitat-biased sampling (Tessarolo et al. 2014). Frequently, species distribution models are calibrated with occurrence data (either presence-only or presence-absence) that are available from heterogeneous sources (e.g. open access databases, distribution atlases, herbarium collections, conservation projects). These data are collected under sampling schemes (survey design and effort level) defined for specific aims at particular spatial scales. Consequently, when used in other contexts and with other aims, they may not be adequate for achieving good model performance, introducing weaknesses related to sampling bias (Soberón and Peterson 2004; Hortal et al. 2007; Guralnick et al. 2007). If occurrence data are environmentally biased towards certain habitats, mostly due to species detectability associated with density, researcher accessibility or conservation priority (Gu and Swihart 2004; Comte and Grenouillet 2013; Lahoz-Monfort et al. 2014), the accuracy of model predictions may be inadequate for conservation applications. For instance, in the case of a species living in forests and grasslands, models calibrated with habitat-biased data (e.g. data collected in forests but not in grasslands) would account for truncated environmental responses. These models would fail when extrapolated to other regions where the two habitats are present (Braunisch et al. 2008; Suárez-Seoane et al. 2014). If habitat-bias sampling is ignored, the fitted model might be closer to a model of survey effort than to a model of the true distribution of the species (Phillips et al. 2009). Avoiding this problem is, therefore, necessary to achieve accurate predictions and can only be reached through a proper sampling design (Peterson and Cohoon 1999).

Another issue that may affect the applicability of distribution models in multi-habitat species conservation is related to stationarity. In SDM, environmental responses are usually considered stationary or identical for the entire dataset (Foody 2004). However, the tendency for any modelled relationship or process is to vary spatially (Osborne et al. 2007). When non-stationary responses are suspected (e.g., in the case of species living in large geographic areas), prior partitioning analyses may be useful to alert the modeller about problems of model extrapolation (Osborne and Suárez-Seoane

2002; Jiménez-Alfaro et al. 2018). In the case of multi-habitat species, environmental responses may change not only geographically within one single habitat, but also among habitats according to differences in resource availability, environmental conditions and biotic interactions (Brambilla and Saporetti 2014; Frans et al. 2018; Maiorano et al. 2019). Indeed, for the case of highly mobile species, environmental responses and habitat use may also vary seasonally, over life-cycle stage (Suárez-Seoane et al. 2008; Zuckerberg 2016). In such cases, habitat-partitioning can be applied to calibration data in order to identify non-stationary responses against environmental factors within the species range. Habitat-partitioning could also allow for dealing with sampling bias, particularly when species data have been collected in specific habitats only.

The explicit consideration of habitat information in SDM approaches dealing with multi-habitat species appears as a potential tool to improve model inference and test non-stationary responses. Habitat is generally considered as a description of the biotic and abiotic nature of the physical place where the organisms of a particular species can live (Mitchell 2005; Kearney 2006). Despite many authors (e.g. Dennis et al. 2003) claim for applying a functional resource-based concept (i.e., a continuum of available resources), information about habitat frequently follows a patch-based definition (i.e., a set of discrete patches showing suitable conditions). At regional scale, habitat information is usually included in SDM as a categorical predictor (e.g. Thuiller et al. 2004a) derived from maps representing discrete patches of vegetation or land cover. Nevertheless, remote sensing data may provide quantitative surrogates of habitat avoiding the uncertainty of patch-based approaches. For example, reflectance data derived from remote sensing techniques play an important role in describing functional attributes of vegetation as a continuum at regional scale (e.g. He et al. 2015; Alcaraz-Segura et al. 2017). Morán-Ordóñez et al. (2012) found that reflectance values from

Landsat TM images were better predictors of mountain plant species´ distribution than other remote sensing products, as spectral indices or vegetation classified maps. Even thought, the interpretation of spectral data in ecological applications is challenging. A promising alternative emerge from the combination of spectral data with categorical vegetation maps in Predictive Vegetation Models (PVMs; Franklin 1995; Chapman and Purse 2011; Tarkesh and Jetschke 2012; Álvarez-Martínez et al. 2018; Jiménez-Alfaro et al. 2018) that may allow the development of continuous, integrative and interpretable predictors of habitat in SDM.

Using as a case study the bilberry (*Vaccinium myrtillus*), a multi-habitat plant species that occurs in three distinct habitats in the Cantabrian Mountains (north-western Spain), we evaluate the role of different types of habitat predictors, along with habitat-partitioning. Our main aims are: (i) to improve SDM performance, generality and extrapolation success; (ii) to assess the stationarity of environmental responses across habitats; and, (iii) to evaluate the impact of habitat-biased calibration on regional map predictions. Our scenarios of data availability reproduce situations where modellers have access only to calibration data collected in some of the habitats where a multi-habitat species can thrive.

Methods

Study case

Bilberry *Vaccinium myrtillus* L. (Ericaceae) is a long-lived, deciduous and rhizomatous shrub that can be found as dominant or co-dominant in a variety of woodlands, shrublands and heathlands throughout cold and temperate regions of Eurasia. In Europe, the species is restricted to poor and moist soils (Coudun and Gégout 2007). It has been demonstrated that bilberry shows morphological and physiological divergence across habitats, differing significantly in terms of plant productivity (Elisabetta et al. 2013), gas exchange and morphology (Woodward 1986), as well as accumulated primary and secondary metabolites in fruits (Mikulic-Petkovsek et al. 2015). However, no difference in clonal diversity and spatial structure of clones has been detected between different habitats (Albert et al. 2004).

The Cantabrian Mountains (NW of Spain) are located at the westernmost distribution limit of the European mountain systems, in a transitional zone between the Atlantic and Mediterranean biogeographic regions. They cover approximately 31,494 km^2, with an altitude ranging from the sea level to 2648 m a.s.l. The climate varies from Temperate-Oceanic (northern slope) to Mediterranean (southern slope). These climatic features, together with the uneven topography and the historical land management, have resulted in a highly heterogeneous landscape that host a wide variety of ecosystems, habitats and endemic species. In these mountains, that have been recognized as a hotspot of biodiversity (Worboys et al. 2010; García-Llamas et al. 2016, 2018, 2019), bilberry has a regional interest as a trophic resource for endangered species, such as the Cantabrian Capercaille (Blanco-Fontao et al. 2009) and the Cantabrian Brown Bear (Rodríguez et al. 2007; Penteriani et al. 2019). The species mainly occurs in acidic vegetation related to northern exposures and can be found across three habitats: acidic woodlands, Atlantic heathlands and alpine dwarf-shrublands (Table 1 and Annex 1 of the Supplementary material).

Species occurrence data

We collected two independent datasets on species occurrence (presence-only data): one for model calibration ("calibration dataset") and the other one for model evaluation ("evaluation dataset"). The calibration dataset consisted of 318 GPS locations (average positional error of 10 meters) that were gathered across the three habitat types where the species occurs in the study area. To build this database we compiled information recorded by different research groups in the context of specific research projects carried out in the study area during the period 2005-2010. These projects were focused on the assessment of: (i) capercaillie leks in acidic woodlands (Segura et al. 2014), (ii) physiological traits of *Vaccinium myrtillus* in alpine dwarf-shrublands (Pato and Obeso 2012) and (iii) distribution patterns of *Calluna vulgaris* in Atlantic heathlands (authors, unpublished data). This heterogeneous calibration dataset was chosen deliberately to show the limitations of using data from other authors that have not been collected specifically for the target research. The evaluation dataset was collected through new fieldwork carried out in 2011-2012 using a model-based sampling (Guisan et al. 2006), by which records were regularly gathered across transects located in areas where a set of preliminary models consistently predicted the highest suitability for the species (see Model calibration section). To achieve the spatial independence of this dataset, sampling was done in areas not surveyed in the calibration step. This dataset comprised 122 GPS locations (average error of 5 meters) where the presence and cover (in percentage) of bilberry was recorded in plots of 30 m x 30 m meters (the spatial resolution of the SDM analyses).

To reduce geographic bias and spatial autocorrelation in both datasets, we carried out spatial filtering, which improves model reliability and inference (Boria et al. 2014; Radosavljevic and Anderson 2014). We used Moran´s I statistic (Moran 1950; Gittleman and Kot 1990; Martins 1996) to test spatial autocorrelation for each environmental predictor (Table 2) in grid sizes of 60, 120, 240 and 480 meters (2, 4, 8 and 16 times the basic spatial resolution of the analysis). We retained the 60 m-rule since the autocorrelation significantly decreased beyond this threshold. After filtering, we kept 148 and 89 records for calibration and evaluation, respectively (Table 1, Figure 1). Data were handled in ArcGIS 10.6 (ESRI 2018).

Topo-climatic and habitat predictors

We prepared a pool of 12 environmental variables to be used in different combination according to the modelling approach (Table 2): five accounting for climate, topography and lithology ("topo-climatic predictors") and seven informing on habitat ("habitat-predictors"). These variables were chosen according to expert knowledge (e.g. Coudun and Gégout 2007) indicating that *Vaccinium myrtillus* is strictly acidic and prefers moist soils in relatively cool locations not subjected to summer drought. In areas of Mediterranean influence, the species is mainly found at relatively high elevation or shady environments. Data were collected at the best spatial resolution available in the study area, considering the characteristics of the species dataset. Predictors were processed in ArcGIS 10.6 (ESRI 2018).

Climate variables (temperature and moisture) were extracted from the Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005), where monthly averaged ground-data collected from available meteorological stations (period 1950–1999) were interpolated (multiple regression in combination with a residual correction method) at 200 m resolution across the Iberian Peninsula. Topography was assessed by means of slope and insolation that were calculated from a digital terrain model at 30 m resolution. The role of lithology was evaluated through a soil pH map at 1 km resolution from ISRIC World Soil Information (www.isric.org), which is the only soil data available for the whole region. Although this spatial resolution is broad, it is important to differentiate between large areas dominated by acid and calcareous soils, given that the species is strictly restricted to acid bedrocks.

Regarding habitat information, we considered three datasets: (i) A categorical habitat map at 1:50.000 scale based on vegetation types (Atlas of Natural and Seminatural Habitats of Spain, year 2005). (ii) Reflectance values of channels 3 and 4 from Landsat TM at 30 m resolution corresponding to June of 2005 (see Morán-Ordóñez et al. 2012 for technical details). Each of these channels provides different information on physical properties of the land surface (red channel 3 discriminates vegetation slopes and near infrared channel 4 emphasizes biomass content) based on the special absorbance behaviour of each terrestrial feature, which is recorded at the different wavelengths of the spectra (0.63-0.69 and 0.76-0.90 micrometres, respectively). (iii) Predicted values (ranging from 0 to 1) computed from predictive vegetation models developed with MaxEnt 3.3.3 (Phillips et al. 2006; Phillips and Dudik 2008) for each target habitat and for all habitats together. PVMs were calibrated using a stratified dataset of 700 points informing on vegetation types (400 for acidic woodlands, 200 for Atlantic heathlands and 100 for alpine dwarf-shrublands, numbers according to the geographic extent of each habitat and the threshold for minimizing autocorrelation). These points were randomly extracted from the Vegetation Map of Asturias at scale 1:25000 (Marquínez et al. 2002). Since sampling effort was constant across the whole habitat map, we created a single background dataset for all PVMs, consisting of 10,000 points randomly distributed within the extent of the vegetation map. As predictors, we used topo-climatic variables and Landsat channels. See Annex 2 of the Supplementary material for further information.

All predictors were rescaled to 30 m, the resolution of the analysis that was constrained by both Landsat satellite imagery and topographic data. To prevent multicollinearity effects, we ran Spearman pairwise correlations in SPSS v.21 (2012) among all predictors over 5000 randomly-selected points, verifying that all were <0.8 (Tabachnick and Fidell 1996).

Model calibration

We used MaxEnt 3.3.3 to model the distribution of *Vaccinium myrtillus*, a method that can provide robust predictions of species occurrence when only-presence data are available at low and moderate sampling size. MaxEnt model specifications for response shapes and regularization choices were chosen by default. We developed four modelling approaches (Table 3). *Approach 1 ("Topo-climate")* was a baseline approach where climate, topography and lithology were used as predictors of species distribution. *Approach 2 ("Additive habitat-map")* was an additive approach where, on the top of the topo-climatic variables, we included the categorical habitat map as a habitat predictor. *Approach 3* ("*Additive Landsat*") was similar but, in this case, habitat predictors were the continuous values of reflectance derived from Landsat imagery (channels 3 and 4). *Approach 4 ("Integrative PVM"*) was an integrative approach where habitat predictors were made of PVM predictions (see previous section). In this approach, only one explanatory variable was entered in each model, according to the habitat being modelled.

For each approach, we ran four models: three "habitat-partitioned models" (each calibrated using the species locations collected in each habitat separately) and one "non-partitioned model" (calibrated with all the occurrence data altogether). All models built for each partitioning option were calibrated with the same species calibration dataset. To deal with sampling bias derived from non-planned surveys, background samples were spatially adjusted to the calibration area. We created four background samples (one for each habitat and altogether) of 10,000 random points each, adjusted to 5 km-grids with bilberry presence (i.e., those including at least one record of the target species). To avoid overprediction (Chefaoui and Lobo 2008), background was not sampled within areas where species is known to be absent because of dispersal limitations and biotic interactions or within areas excluded from model calibration (Anderson and Raza 2010; Barve et al. 2011; Kramer-Schadt et al. 2013; Radosavljevic and Anderson 2014).

For each model output, we extracted the fractional predicted area (FPA) as the proportion of cells predicted to have suitable habitat for the target species according to different thresholds of suitability.

The spatial congruence between spatial outputs was evaluated by means of bivariate correlations that were calculated in a set of 3000 random points using the library “corrplot” in R software (R Core Team 2019).

Model evaluation

We quantified model performance, overfitting and extrapolation ability for all modelling approaches. Model performance was measured as the discriminatory ability of the model that, in presence-background SDM techniques, is the degree to which a model scores species occurrence data higher than background sites (Phillips et al. 2009). Discriminatory ability was evaluated using two threshold-independent methods fairly insensitive to species prevalence (Franklin 2009): the AUC (area under the receiver operating characteristic curve) adapted for use with background samples and the Boyce index (Boyce et al. 2002; Hirzel et al. 2006). It should be noted that AUC values calculated in MaxEnt vary with the fractional predicted area and, therefore, they are not comparable among species or across regions. However, the models developed in this study correspond to the same species and are evaluated in the same study region, which make AUC values suitable for comparison (Lobo et al. 2008). To allow for more reliable estimates, we always compared groups of models by using the same dataset, so that the measured performance has the same meaning (Suárez-Seoane et al. 2014). AUC values were interpreted according to Swets (1988): 0.90–1.00: excellent, 0.80–0.90: good, 0.70–0.80: fair, 0.60–0.70: poor and 0.50–0.60: fail. The Boyce index measures the Spearman rank correlation coefficient between the frequency of presence locations within ranked classes of predicted habitat suitability (adjusted by area) and the mean habitat suitability of these classes. It ranges from -1 to +1. Negative values indicate an incorrect model which predicts poor quality areas where the species is more frequent; positive values indicate a model whose predictions are consistent with species occurrence patterns in the evaluation dataset. To evaluate model performance, we followed the next procedures: (i) Simple re-substitution (Fielding and Bell 1997), where AUC values were calculated against the same data used for calibration, with no independence. This technique may yield to inflated estimates of performance, but is the easiest procedure to evaluate how well a model fits the data from which it was derived. (ii) Statistical resampling, where AUC values were calculated by performing 5-fold cross-validation. Resampling reduces the bias in the assessment of model performance. It is used to avoid overfitting by halting model growth based on predictive accuracy on withheld portions of the data (Phillips et al. 2009). (iii) Independent field validation, where AUC and Boyce values were quantified on the evaluation dataset. Using evaluation data spatially independent from calibration data allows for more accurate estimates of model performance, overfitting and extrapolation (Peterson et al. 2011; Radosavljevic and Anderson 2014). Complementarily, we used the evaluation dataset to calculate the Spearman correlations between *Vaccinium myrtillus* cover estimated in the field and model predictions (Jiapaer et al. 2011; Zhang et al. 2013).

Overfitting, as a proxy of model generality, was quantified using the methodology described in Radosavljevic and Anderson (2014) (see also Warren and Seifert 2011): (i) Subtracting the difference between calibration and evaluation AUCs, which is a threshold-independent measure. (ii) Comparing both observed and theoretical levels of omission for the evaluation dataset, using two thresholds: the “Minimum Training Presence Threshold” (MTPT; the lowest predicted value for an evaluation locality) and the “10 Percentile Training Presence” (10PTP; the value that excludes the 10% of the localities with the lowest predicted values). The best results are those that approach zero for MTPT and 10 for 10PTP because they reflect perfect predictions. The higher is the value with respect to zero and 10, respectively, the higher is model overfitting, thus suggesting lower model accuracy.

To evaluate the extrapolation success of habitat-partitioned models outside their calibration area (i.e., in the whole study area), we calculated, for each modelling approach, the AUC values against the full evaluation dataset that includes bilberry locations in all habitats. Complementarily, we quantified, for the evaluation dataset, the observed and theoretical levels of omission of each habitat-partitioned model using both the MTPT and 10PTP thresholding rules. This extrapolation analysis also allowed for assessing the impact of using habitat-biased calibration data on model predictions for the whole area and identify non-stationary responses. If environmental responses vary among habitats, the extrapolation success is expected to be low. The stationarity of the environmental responses among habitats was further explored by means of: (i) response curves (testing both marginal and independent effects); and, (ii) relative contribution of each predictor (estimated as the permutation importance values) to the models. Analyses were carried out using MaxEnt 3.3.3 (Phillips et al. 2006) and SPSS v.21 (2012).

Results

As a general trend, models had a good discriminatory ability (AUC above 0.8) and showed low levels of overfitting, either considering the habitats separately or altogether (Table 4). Regarding non-partitioned models, approaches including habitat predictors always achieved higher performance (predictions fitted the calibration and evaluation datasets at best; see values of AUC in Approach 3) and correlated better with bilberry cover (see Approach 4) than the baseline Approach 1. Overfitting was generally low in all approaches, being the lowest values for the baseline model. Looking at the habitat-partitioned models, including habitat predictors increased model discrimination in respect to the baseline approach for the case of Atlantic heathlands and acidic woodlands (see Approach 3), but not for alpine dwarf-shrublands. Habitat data also allowed for achieving a better correlation between model predictions and bilberry cover (Approaches 2 and 4), as well as a reduction of the overfitting for all the habitats, particularly in the case of Approach 4.

The visual inspection of the logistic outputs revealed similar spatial patterns of distribution across modelling approaches, but important differences between habitats (see Annex 3 of the Supplementary material). Figure 2 includes the spatial outputs derived from Approach 3, as an example. When both the MTPT and 10PTP thresholding rules were applied, the fractional predicted area (FPA) identified for Approaches 2 and 3 was generally the lowest (Figure 3).

The success of extrapolating the habitat-partitioned models to the overall study area varied widely with habitat and modelling approach (Table 5), but it was generally low (most AUC values ranged from 0.50 to 0.78, one model performed 0.34). The highest discrimination was found for the baseline Approach 1 (AUC: 0.60-0.78) and the alpine dwarf-shrublands. Omission was generally high, but varied among approaches and habitats.

The curve shape and the relative contribution of predictors to the models soundly varied across habitats, being consistent among approaches (Table 6 and Annex 4 of the Supplementary material). In all cases, except for woodlands, temperature was the main predictor for bilberry distribution. Nevertheless, habitat map and satellite channels were, when considered, generally among the top contributing variables, ousting in some cases the effect of temperature (e.g. Approach 3 for acidic woodlands).

Discussion

This study highlights the implications of considering habitat predictors and habitat-partitioning in the calibration of multi-habitat species distribution models. In the case of non-partitioned models, the inclusion of habitat predictors (Approaches 2, 3 and 4) produced more discriminative, but more overfitted models than the baseline Approach 1 based on topo-climatic variables only. However, the low omission rate found for Approach 1 was at the cost of predicting the highest fractional area (estimated with the 10PTP threshold), which might be associated to higher commission rates than approaches including habitat. In contrast, the most restricted suitable area was predicted by Approach 3 at the cost of increasing the omission rate, but reducing the commission rate. These differences in the amount of predicted area can be interpreted in terms of ecological niche. While the baseline model represents a higher proportion of the bilberry fundamental niche and, therefore, of the potential distribution of the species in the study area, the addition of habitat data informing on vegetation and, indirectly, on biotic interactions (Wisz et al. 2013) allows the discrimination of a higher fraction of the realized niche, which is a better surrogate of species real occupancy. This can be inferred from the large differences in model outputs that were found between woodlands and heathlands, reflecting bilberry occupation of different niches in distinct habitats where competition interactions vary soundly, being part either of the woodland understory or the shrub community (Pato et al. 2016), respectively.

When computing habitat-partitioned models, approaches including habitat predictors allowed for achieving more discriminative models than the baseline Approach 1 in the case of acidic woodlands and Atlantic heathlands, but not in alpine dwarf-shrublands. The relevance of considering habitat data for predicting bilberry distribution should be also interpreted in the context of species relative abundance across different habitats. Bilberry is a relatively common species in favourable habitats of the study area (Naves et al. 2018; García-Llamas et al. 2019) and, especially, in acidic woodlands. Thus, it is coherent that approaches incorporating habitat predictors achieve the best results. In the case of alpine dwarf-shrublands, bilberry is clearly restricted to the highest elevations in the study area, which can be easily predicted with topo-climatic factors only. Therefore, using habitat predictors in this case had few advantages when compared to the baseline model.

Our results evidenced the low success of extrapolating habitat-partitioned models outside the calibration area. Although a few models had a fair performance (0.70-0.78), many other performed poorly (0.60-0.70) or randomly (0.51). One specific case even showed a response worse than random (0.34). This finding can be related to: (i) the environmental incompleteness of the calibration dataset; (ii) the non-stationarity of the environmental responses; and / or (iii) the heterogeneity of the calibration dataset, where each data subset may have a different quality, affecting model performance and extrapolation. Environmental completeness is the ability of occurrence data to adequately represent the environmental complexity within the species' geographic distribution (sensu Kadmon et al. 2003; Hortal et al. 2008). It is achieved when samples represent the full range of environmental factors where the species can live. Models calibrated with incomplete species occurrence data (habitat-biased data) may fail to account for the full range of environmental factors of the species and, therefore, they can lead to the estimation of truncated responses (Anderson and Raza 2010), producing inflated estimates of model performance (Veloz 2009) and high rates of overfitting. This reduces the possibility of extrapolating model predictions to other contexts (Thuiller et al. 2004b; Zurell et al. 2012; Peterson et al. 2011; Radosavljevic and Anderson 2014), decreasing their applicability (Randin et al. 2006; Menke et al. 2009; Suárez-Seoane et al. 2014).

Our results also highlight a main role of non-stationary responses (Boakes et al. 2010) that should be specifically addressed in the case of multi-habitat species (Annex 4 of the Supplementary material). The higher is the complexity of the species distribution among habitats, the higher is the chance of having multiple responses across these habitats. Even so, in SDM approaches, species responses are commonly assumed as similar across regions. In our study, this problem was exacerbated since calibration occurrence data were collected in each habitat under different sampling schemes not specifically designed for the current purpose. These results suggest that dealing with multi-habitat SDM requires a careful prior assessment of habitat bias and quality in the occurrence dataset used for calibration.

Despite the general success of our habitat-based approaches, some considerations about data sources should be taken in account. Although incorporating categorical maps as surrogates of habitat (Approach 2) enhances the reliability of SDM, some constraints remain for generalizing their use. First, their availability is limited to particular scales that may not match the requirements of the study (Franklin et al. 2000). Second, physical boundaries of habitats commonly transcend administrative boundaries adopted for mapping purposes. Using regional maps in multi-regional projects may be problematic, since the same habitat patch could be mapped differently according to conceptual and methodological author-specific criteria. Third, companion or even co-dominant species are rarely used to distinguish between habitat categories. Consequently, researchers need a good knowledge on the ecology of the target species to identify the list of habitat classes where it may be present. Fourth, categorical maps are subject to vagueness, which is a type of linguistic uncertainty that typically appears when using arbitrary sharp boundaries to define classes. This problem is inherent to any process involving qualitative reasoning and it is usually solved by using fuzzy logic approaches, where habitat types are understood as intrinsically arbitrary subdivisions of continuous patterns (Elith et al. 2002). On the other hand, the reflectance values used in Approaches 3 and 4 allowed for improving model accuracy and refining the mapped predictions. Since reflectance values provide a direct spectral signal of the vegetation, they may help in distinguishing among vegetation types and offer additional species-specific information (Morán-Ordoñez et al. 2012). Regardless the advantages of using continuous spectral data against categorical information, some general constraints should be mentioned, as the ecological interpretation of these values (they do not account for vegetation or land cover directly) and the error and uncertainty associated to atmospheric influences and vegetation phenology (García-Llamas et al. 2016). Finally, we highlight the potential use of quantitative predictions derived from PVMs as unique predictors (Approach 4). This habitat surrogate provides the response of a given vegetation type that is supposed to be relevant for the species, thus indirectly reflecting its specificity to that habitat (assuming this will be a model product subject to its own assumptions and limitations).

Implications for conservation

This study provides a good example of the implications of considering habitat predictors and habitat partitioning when modelling the distribution of a multi-habitat species. In the study area, bilberry is a key foraging resource for endangered vertebrate species that make a differential use of it across habitats. In fact, during the summer and autumn, bilberry becomes the essential food item for both Cantabrian brown bear (Naves et al. 2006) and Cantabrian capercaille (Rodríguez and Obeso 2000). However, the relative abundance (and, therefore, the availability for consumers) of bilberry may vary between habitats across space and time, which can be critical for these species at this period of the year. Therefore, the achievement of accurate spatial products informing on spatial and temporal variation of key trophic resources is essential for developing realistic conservation strategies at regional scale. Comparing our results with a recent prediction made for the target species in the study area on the basis of forestry occurrence and climatic data (Penteriani et al. 2019), we found that using habitat predictors (including habitat maps or remote sensing data) in partitioned models allowed for achieving spatial products with higher spatial precision at regional scale. While the use of remote sensing data reflects more accurately the local area of occupancy (Álvarez-Martínez et al. 2018), the use of habitat maps and bedrock layers allows for removing limestone-dominated areas, which could have been overlooked when using only topo-climatic variables.

Our results also give insights for other case studies where the target species occurs in more than one distinct habitat. Researchers and conservation managers may be interested in the evaluation of the actual (rather than potential) occurrence of focal species in habitats which are ecologically or structurally different (e.g. heathlands *vs*. forests). The advantages of incorporating habitat predictors in habitat-partitioned models are not only linked to model performance or generality, but also to the reliability of predictions in conservation planning. Maps resulting from these models can help in conservation planning about habitat-specific management practices according to temporal variation in the use of different habitats (Brambilla and Saporetti 2014; Frans et al. 2017; Zuckerberg et al. 2019). We also suggest that using remote sensing data, alone or in combination with vegetation maps, provide relevant information for linking species distributions with the habitat they actually occupy in nature. In any case, decisions about the best modelling approach will depend on the specificity of the final applications, which would require characterising the range of the species at different levels of generality, implying different trade-offs between omission and commission rates.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1. Main habitat types where *Vaccinium myrtillus* occurs in the Cantabrian Mountains and datasets used for model calibration and evaluation (the number of records after spatial filtering is in bold, while the number of records before filtering is shown in parentheses).

	alpine dwarf-shrublands	Atlantic heathlands	acidic woodlands
European Habitat Classification System- EUNIS (Davies et al. 2004)	F2.2	F4.1, F4.2	G1.6, G1.8, G1.9
European Habitats Directive 92/43/EEC (Anon 1992)	4060	4020	9120
Vegetation type (Rodwell et al. 2002)	*Juniperion nanae*	*Daboecion cantabricae*	*Ilici-Fagion*
Dominant species	*Juniperus communis, Vaccinium uliginosum*	*Calluna vulgaris*	*Fagus sylvatica, Quercus petraea, Betula celtiberica*
Calibration datasets	**25** (83)	**19** (49)	**104** (186)
Evaluation datasets	**14** (20)	**45** (71)	**30** (31)

Table 2. Environmental predictors used for modelling *Vaccinium myrtillus* distribution.

Type	Variable	Description	Source
Climate	Tempdd	Temperature degree days: Daily mean temperature > 0ºC x number of days (in ºC.d.yr-1)	Digital climatic Atlas of the Iberian Peninsula at 200 m resolution (Ninyerola et al. 2005)
	Moist	Moisture index: Water balance model for computing the mixed effect of monthly precipitation and evaporation, from 0 (dry) to 1 (saturated)	
Topography	Slope Insolation	Slope (in degrees) Annual solar radiation (in wmj)	DTM at 30m
Lithology	pH	Relative soil pH values	ISRIC World Soil Information at 1 km resolution (http://www.isric.org/)
Habitat	Habmap	Categorical habitat map (119 classes)	Atlas of Natural and Seminatural Habitats of Spain, year 2005, scale 1:50000 (www.magrama.gob.es)
	Channel3	Reflectance values of channel 3 (red wavelength)	Landsat TM at 30m resolution, year 2005 (see Morán-Ordóñez et al. 2011, 2012 for technical details)
	Channel4	Reflectance values of channel 4 (near infrared wavelength)	
	PVM$_{\text{pred-alpine}}$, PVM$_{\text{pred-atlantic}}$, PVM$_{\text{pred-woodland}}$, PVM$_{\text{pred-all}}$	Predictions from predictive vegetation models (PVMs) calculated per habitat and altogether, according to each case (suitability index ranging from 0 to 1)	Own elaboration based on the Vegetation Map of Asturias,1:25,000 scale (Marquínez et al. 2002)

Table 3. Modelling approaches. See Table 2 for code meaning.

	Approach 1 Topo-climate	Approach 2 Additive habitat-map	Approach 3 Additive Landsat	Approach 4 Integrative PVM
Calibration				
Species occurrence data	Calibration datasets: (i) all data, (ii) alpine dwarf-shrublands, (iii) Atlantic heathlands, (iv) acidic woodlands			
Background	Adjusted to 5x5km grids with bilberry presence: One background per each species dataset (i to iv)			
Layers	Tempdd, Moist, Slope, Insolation, pH	Tempdd, Moist, Slope, Insolation, pH, Habmap	Tempdd, Moist, Slope, Insolation, pH, Channel3, Channel4	$PVM_{pred\text{-}alpine}$, $PVM_{pred\text{-}atlantic}$, $PVM_{pred\text{-}woodland}$, $PVM_{pred\text{-}all}$
Output maps				
	Four maps (HSI) per approach: all habitats, alpine heathlands, Atlantic heathlands, acidic woodlands			
Evaluation				
Evaluation data	Evaluation datasets: (i) all data, (ii) alpine dwarf-shrublands, (iii) Atlantic heathlands, (iv) acidic woodlands			

Table 4. Discrimination and overfitting achieved by non-partitioned and habitat-partitioned models within the calibration area under different approaches. AUC: area under the curve; CV: cross-validated models; MTPT: minimum training presence threshold; 10PTP: 10-percentile training presence threshold; Spearman$_{\text{HSI-cover}}$: Spearman correlations between model predictions (habitat suitability index, HSI) and *Vaccinium myrtillus* cover estimated in the field. Values corresponding to the highest performance and lowest overfitting are highlighted in bold.

		Approach 1 Topo-climate	Approach 2 Additive habitat-map	Approach 3 Additive Landsat	Approach 4 Integrative PVM
	“Non-partitioned models” *(all habitats)*				
Discrimination	AUC$_{\text{calibration}}$	0.84	0.89	**0.90**	0.86
	AUC-5CV$_{\text{calibration}}$	0.80±0.04	0.84±0.03	**0.86±0.04**	**0.86±0.03**
	AUC$_{\text{evaluation}}$	0.82	**0.85**	0.81	0.80
	Boyce$_{\text{evaluation}}$	0.43	0.98	**1.00**	0.01
	Spearman$_{\text{HSI-cover}}$	0.11	0.03	0.18	**0.31**
Overfitting	AUC$_{\text{calibration}}$ - AUC$_{\text{evaluation}}$	**0.01**	0.04	0.08	0.06
	Omission rate$_{\text{evaluation}}$ (MTPT)	**0.00**	0.03	0.06	0.07
	Omission rate$_{\text{evaluation}}$ (10PTP)	**0.17**	0.17	0.24	0.18
	“Habitat-partitioned models” *(alpine dwarf-shrublands)*				
Discrimination	AUC$_{\text{calibration}}$	0.97	0.97	0.97	0.93
	AUC-5CV$_{\text{calibration}}$	**0.96±0.02**	0.95±0.03	**0.96±0.02**	0.92±0.05
	AUC$_{\text{evaluation}}$	**0.95**	0.93	0.92	0.88
	Boyce$_{\text{evaluation}}$	**0.37**	0.35	0.25	0.28
	Spearman$_{\text{HSI-cover}}$	-0.31	-0.47	-0.01	**0.10**
Overfitting	AUC$_{\text{calibration}}$ - AUC$_{\text{evaluation}}$	**0.02**	0.05	0.05	0.05
	Omission rate$_{\text{evaluation}}$ (MTPT)	0.07	0.07	0.14	**0.00**
	Omission rate$_{\text{evaluation}}$ (10PTP)	0.21	0.29	0.21	**0.14**
	“Habitat-partitioned models” *(Atlantic heathlands)*				
Discrimination	AUC$_{\text{calibration}}$	0.95	0.95	**0.97**	0.91
	AUC-5CV$_{\text{calibration}}$	0.93±0.04	0.91±0.07	**0.94±0.04**	0.90±0.05
	AUC$_{\text{evaluation}}$	0.85	0.82	**0.86**	0.82
	Boyce$_{\text{evaluation}}$	0.47	-0.17	**0.64**	-0.36
	Spearman$_{\text{HSI-cover}}$	0.13	-0.02	0.18	**0.33**
Overfitting	AUC$_{\text{calibration}}$ - AUC$_{\text{evaluation}}$	0.11	0.12	0.11	**0.09**
	Omission rate$_{\text{evaluation}}$ (MTPT)	0.19	**0.13**	0.27	0.27
	Omission rate$_{\text{evaluation}}$ (10PTP)	0.46	0.70	0.51	**0.27**
	“Habitat-partitioned models” *(acidic woodlands)*				
Discrimination	AUC$_{\text{calibration}}$	0.85	0.91	**0.92**	0.88
	AUC-5CV$_{\text{calibration}}$	0.79±0.04	0.87±0.06	**0.88±0.03**	0.87±0.02
	AUC$_{\text{evaluation}}$	0.76	**0.83**	**0.83**	0.81
	Boyce$_{\text{evaluation}}$	0.00	**0.20**	-0.04	**-0.24**
	Spearman$_{\text{HSI-cover}}$	-0.05	**0.20**	0.09	0.12
Overfitt	AUC$_{\text{calibration}}$ - AUC$_{\text{evaluation}}$	0.09	0.08	0.09	**0.07**
	Omission rate$_{\text{evaluation}}$ (MTPT)	0.10	0.12	**0.07**	**0.07**
	Omission rate$_{\text{evaluation}}$ (10PTP)	0.27	0.35	0.27	**0.20**

Table 5. Extrapolation of habitat-partitioned models across the study area (validated with the "testing dataset" containing locations from all habitats). AUC: area under the curve; MTPT: "minimum training presence threshold"; 10PTP: "10-percentile training presence threshold".

Habitat-partitioned models		Approach 1 Topo-climate	Approach 2 Additive habitat-map	Approach 3 Additive Landsat	Approach 4 Integrative PVM
Alpine heathlands	$\text{AUC}_{\text{testing}}$	**0.78**	0.68	0.75	0.75
	MTPT	0.38	0.31	0.45	**0.28**
	10PTP	0.64	0.76	0.64	**0.41**
Atlantic heathlands	$\text{AUC}_{\text{testing}}$	**0.71**	0.68	0.69	0.66
	MTPT	0.41	**0.31**	0.53	0.49
	10PTP	0.63	0.76	0.72	**0.49**
Acidic woodlands	$\text{AUC}_{\text{testing}}$	**0.60**	**0.60**	0.51	0.34
	MTPT	**0.17**	0.31	0.49	0.69
	10PTP	**0.41**	0.78	0.76	0.74

Table 6. Environmental responses of the target species across habitats and approaches. The table shows the relative contribution of each predictor to each MaxEnt model estimated as the permutation importance values (i.e., the values of each predictor on the training presence and background datasets are randomly permuted, the model is re-evaluated on the permuted data and the resulting drop in training AUC is calculated and normalized to percentage values). The shape of the marginal curves representing how the predicted suitability changes as each environmental variable is varied (keeping all other environmental variables at their average sample value) is shown between parentheses (L =linear, E =exponential, S =sigmoidal, Q =quadratic) and sign (+ =Positive, - =Negative, 0 =Flat). See Table 2 for variable description.

	Approach 1 Topo-climate		Approach 2 Additive habitat-map		Approach 3 Additive Landsat		Approach 4 Integrative PVM	
"Non-partitioned models" *(all habitats)*								
Tempdd	**40.3**	(E-)	**47.8**	(E-)	**46.8**	(E-)	-	-
Moist	**21.0**	(L+)	3.5	(S)	5.8	(L+)	-	-
Slope	3.6	(L+)	6.6	(S)	2.4	(L+)	-	-
Insolation	**26.8**	(Q+)	**25.8**	(Q+)	7.7	(Q+)	-	-
pH	8.2	(L+)	1.7	(S)	5.1	(S)	-	-
Habmap	-	-	**14.6**	-	-	-	-	-
Channel3	-	-	-	-	**29.5**	(E-)	-	-
Channel4	-	-	-	-	2.6	(Q+)	-	-
PVM$_{pred-all}$	-	-	-	-	-	-	**100**	(S)
"Habitat-partitioned models" *(Alpine heathlands)*								
Tempdd	**82.0**	(E-)	**77.5**	(E-)	**77.9**	(E-)	-	-
Moist	4.7	(S)	1.4	(S)	5.6	(S)	-	-
Slope	0	(S)	0.3	(S)	0	(S)	-	-
Insolation	2.9	(E-)	3.5	(E-)	2.6	(E-)	-	-
pH	**10.4**	(S)	9.6	(S)	**11.3**	(S)	-	-
Habmap	-	-	7.8	-	-	-	-	-
Channel3	-	-	-	-	2.5	(Q+)	-	-
Channel4	-	-	-	-	0	(E-)	-	-
PVM$_{pred-alpine}$	-	-	-	-	-	-	100	(S)
"Habitat-partitioned models" *(Atlantic heathlands)*								
Tempdd	**65.0**	(E-)	**77.0**	(E-)	**54.4**	(E-)	-	-
Moist	5.4	(Q-)	1.2	(L-)	0.7	(S)	-	-
Slope	**17.3**	(E-)	**13.3**	(E-)	**14.0**	(E-)	-	-
Insolation	5.5	(Q+)	0	Flat	4.2	(Q+)	-	-
pH	6.9	(S)	0	(S)	9.0	(S)	-	-
Habmap	-	-	8.5	-	-	-	-	-
Channel3	-	-	-	-	1.7	(E-)	-	-
Channel4	-	-	-	-	**16.0**	(E-)	-	-
PVM$_{pred-atlantic}$	-	-	-	-	-	-	**100**	(S)
"Habitat-partitioned models" *(acidic woodlands)*								
Tempdd	**28.5**	(Q+)	**14.2**	(Q+)	**15.2**	(Q+)	-	-
Moist	**21.9**	(S)	0.3	(S)	2.9	(S)	-	-
Slope	1.6	(E+)	4.3	(S)	1.5	(S)	-	-
Insolation	**35.9**	(Q+)	**41.8**	(E-)	6.2	(Q+)	-	-
pH	**12.2**	(S)	2.5	(E-)	7.7	(S)	-	-
Habmap	-	-	**36.9**	-	-	-	-	-
Channel3	-	-	-		**56.4**	(E-)	-	-
Channel4	-	-	-		**10.1**	(Q+)	-	-
PVM$_{pred-woodland}$	-	-	-	-	-	-	**100**	(S)

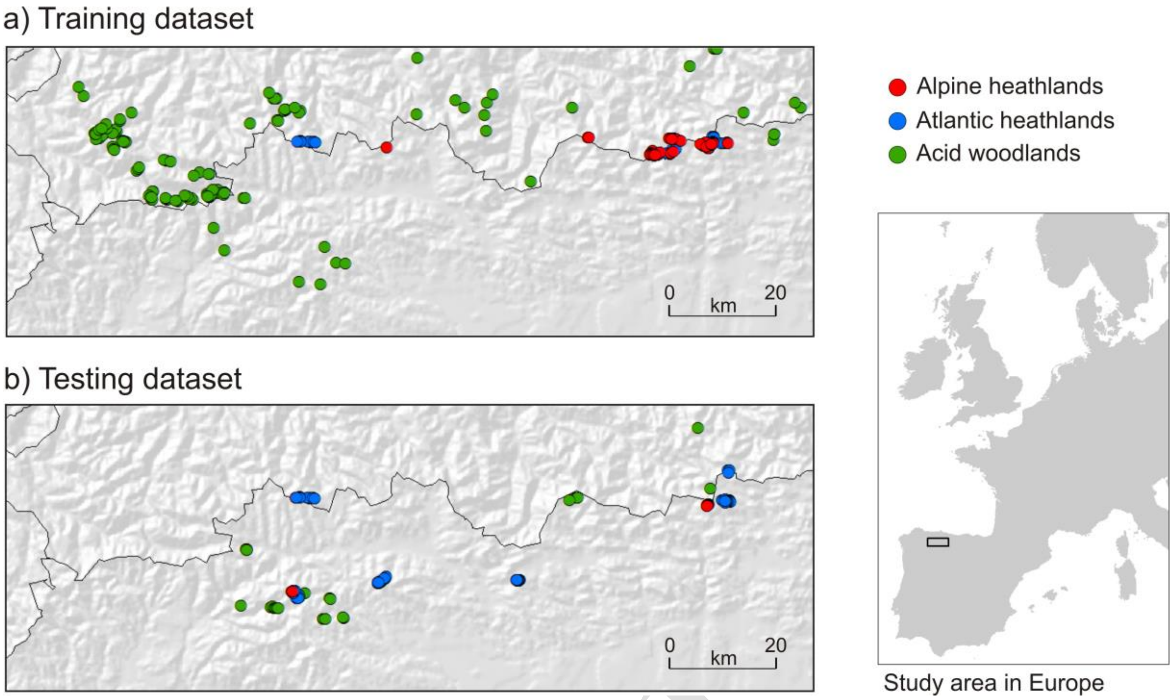
List of figures

Fig. 1. Study area.

Fig. 2. Logistic outputs (habitat suitability index) of MaxEnt for Approach 3. (a) “Non-partitioned model”: all habitats. “Habitat-partitioned models”: (b) alpine dwarf-shrublands, (c) Atlantic heathlands and (d) acidic woodlands. Values range from 0 (white colour) to 1 (black colour).

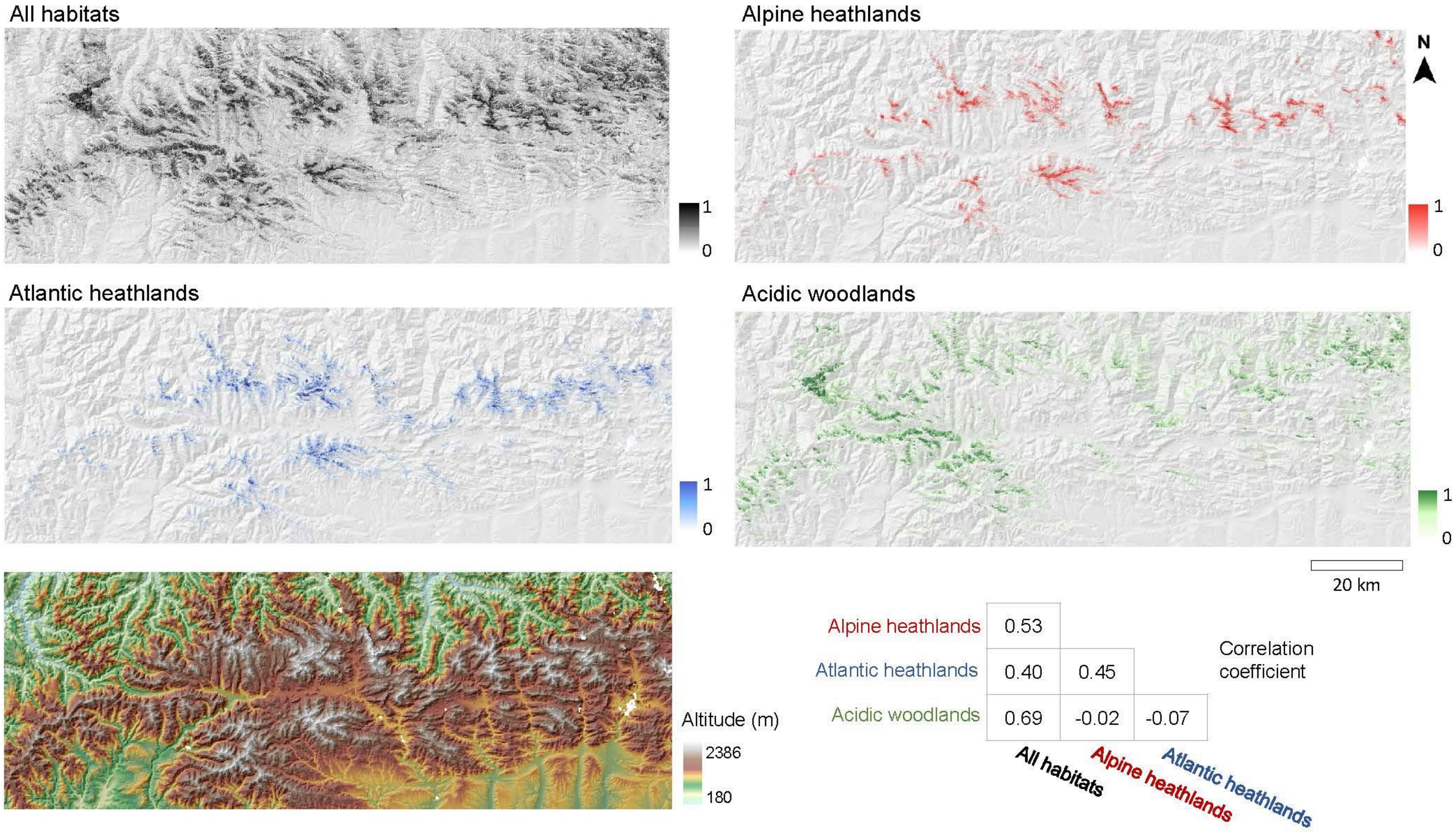
Fig. 3. Fractional predicted area (FPA; proportion of cells predicted to have suitable habitat for the target species), in percentage, according to different thresholds: “Minimum Training Presence Threshold” of MaxEnt (MTPT) and the “10 Percentile Training Presence” (10PTP). Numbers 1 to 4 correspond to the approaches: (1) topo-climate, (2) additive habitat map, (3) additive Landsat, (4) integrative PVM.

Fig. 1


a) Training dataset

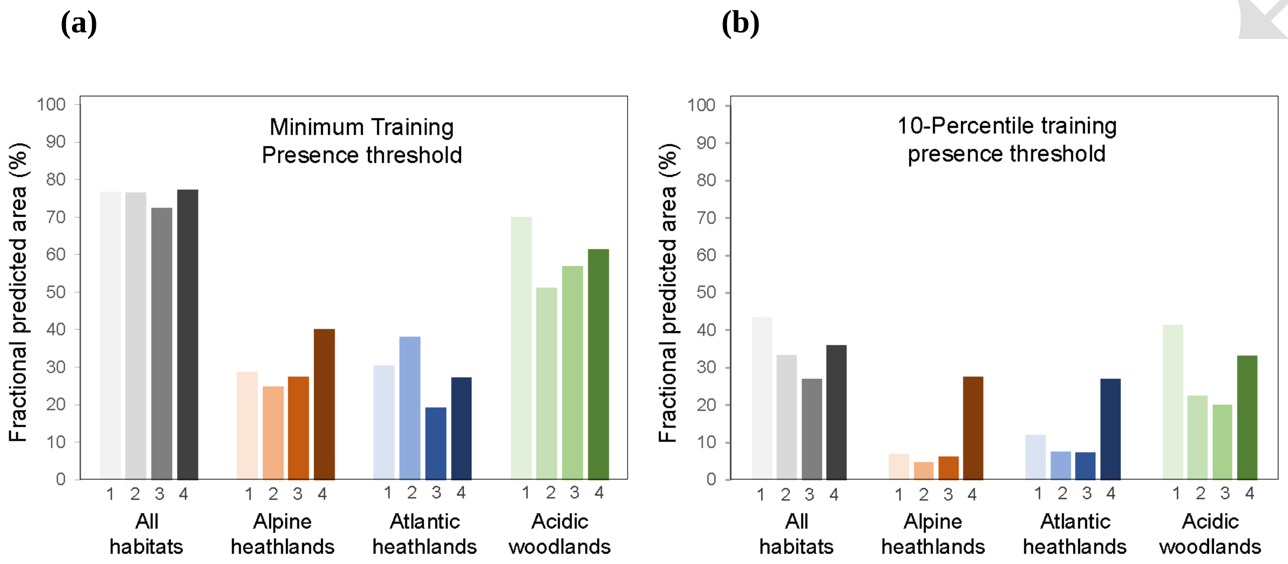
b) Testing dataset

Fig. 2

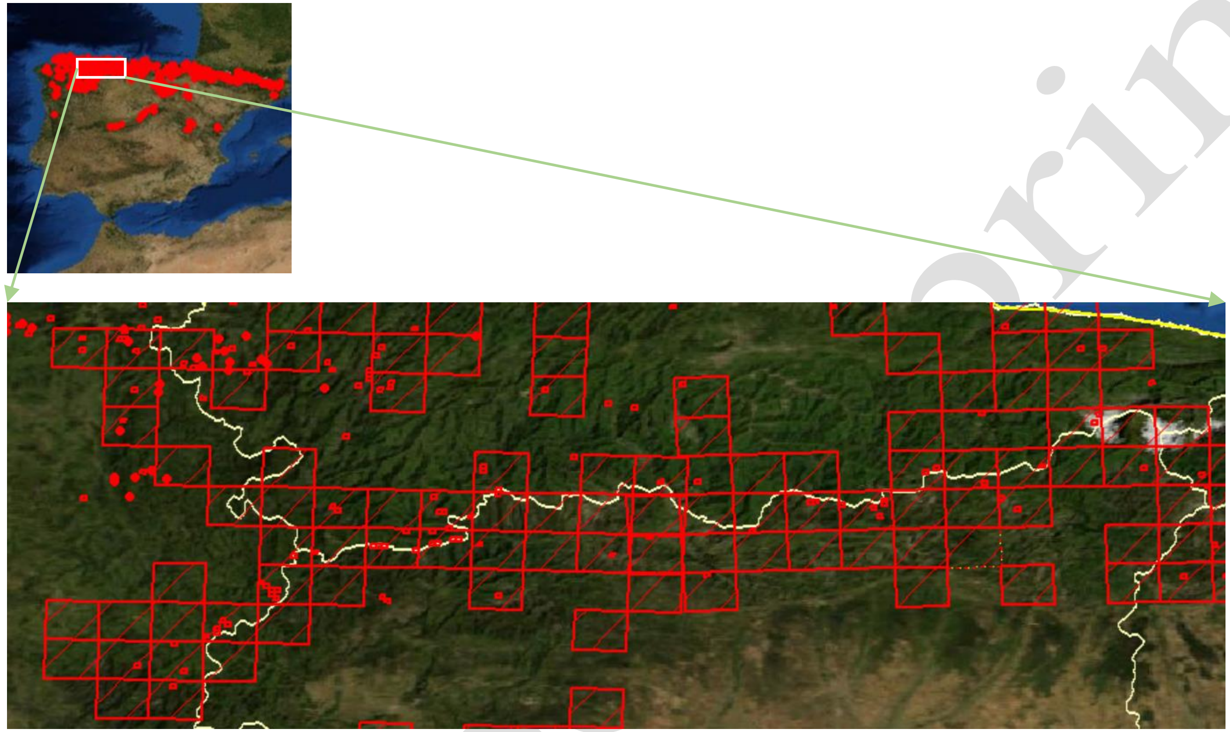


	All habitats	Alpine heathlands	Atlantic heathlands
Alpine heathlands	0.53		
Atlantic heathlands	0.40	0.45	
Acidic woodlands	0.69	-0.02	-0.07

Fig. 3

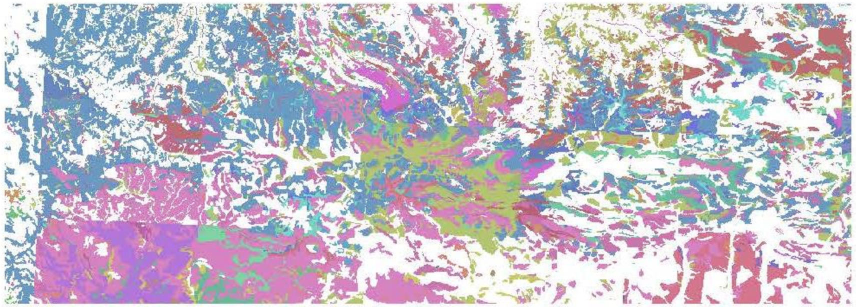

(a)
(b)
Minimum Training Presence threshold
10-Percentile training presence threshold
Fractional predicted area (%)
0
10
20
30
40
50
60
70
80
90
100
1 2 3 4
All habitats
Alpine heathlands
Atlantic heathlands
Acidic woodlands

Supplementary material- Annex 1. Distribution range of *Vaccinium myrtillus* in the Iberian Peninsula and, particularly, in the study area (Cantabrian range) according to ANTHOS database (www.anthos.es, accessed October 2019). Large and small quadrats reflect species occurrence in 10 km x 10 km and 1km x 1 km grids, respectively.

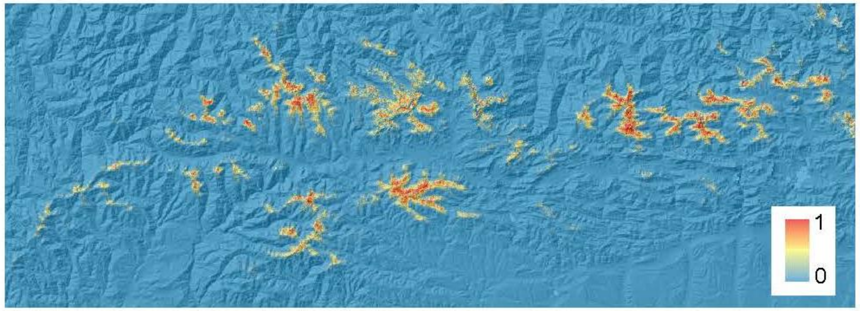


Supplementary material- Annex 2. Habitat predictors used in model calibration.

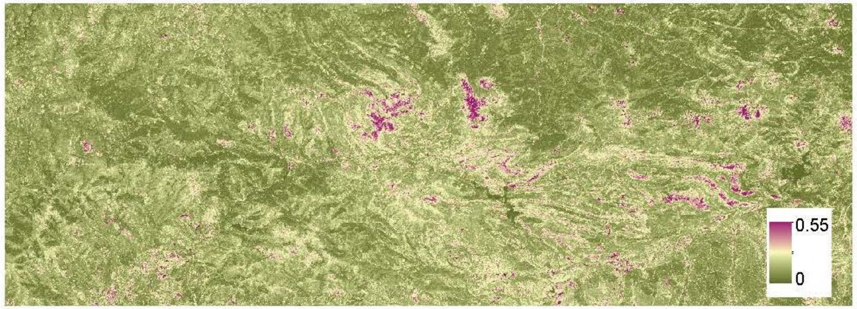
Vegetation map of natural habitats (scale 1:50.000)



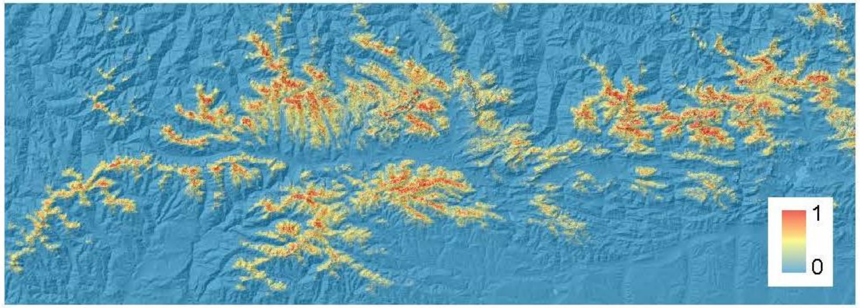
PVM Alpine heathlands



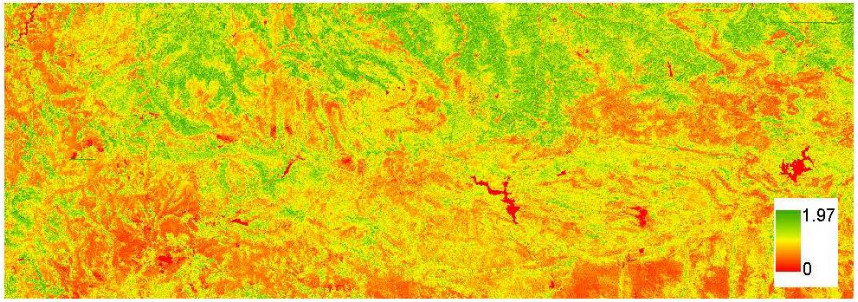
Landsat channel 3 (vegetation slopes)



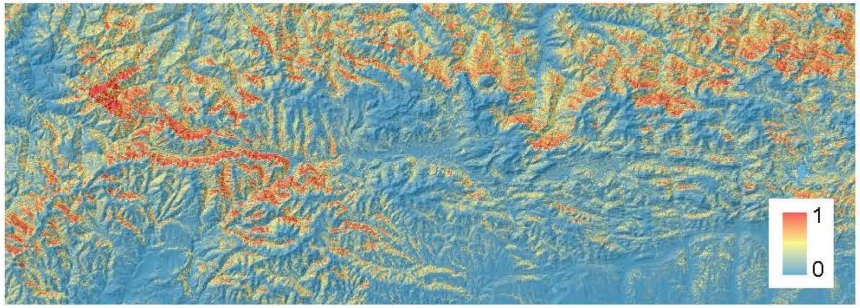
PVM Atlantic heathlands



Landsat channel 4 (biomass content)



PVM Acidic woodlands

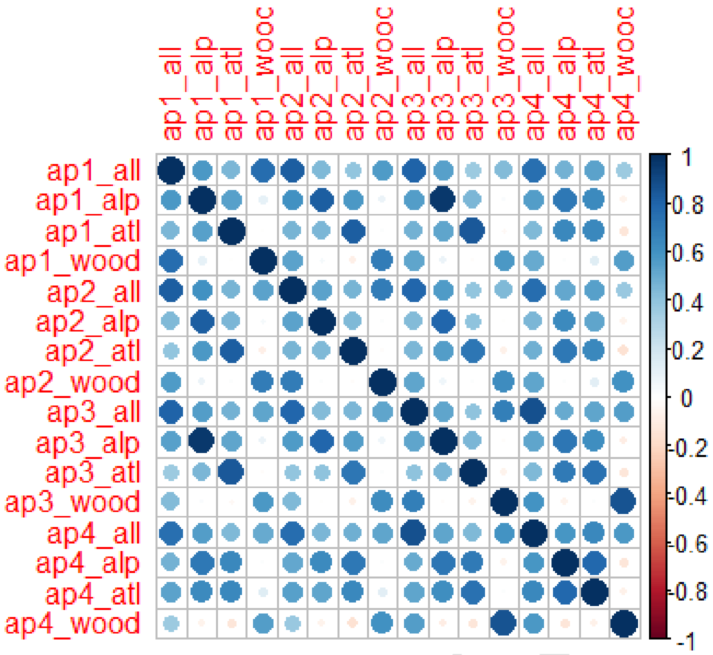


PVM modelling approach

Predictive Vegetation Models (PVMs) were calibrated using: (i) A stratified random dataset of 700 occurrence points (only one observation per 30m grid cell, the spatial resolution of the analysis) informing on vegetation type, collected across the Vegetation Map of Asturias at scale 1:25000 (Marquínez et al. 2002): 400 for acidic woodlands, 200 for Atlantic heathlands and 100 for alpine dwarf-shrublands. (ii) A single background dataset (sampling effort was constant across the whole habitat map) of 10,000 points randomly distributed within the extent of the vegetation map that encompasses the prediction locations and informs on the distribution of the covariates in the landscape. (iii) A set of topo-climatic (temperature, moisture, slope, insolation and pH, likely influencing the occurrence of different vegetation types) and satellite variables (red and near infrared Landsat channels) that were included as vegetation predictors. To minimize further multi-collinearity problems, we checked that Spearman pairwise correlations between all candidate predictors were <0.8 in a sample of 50000 points randomly distributed across the study area (Tabachnick and Fidell 1996).

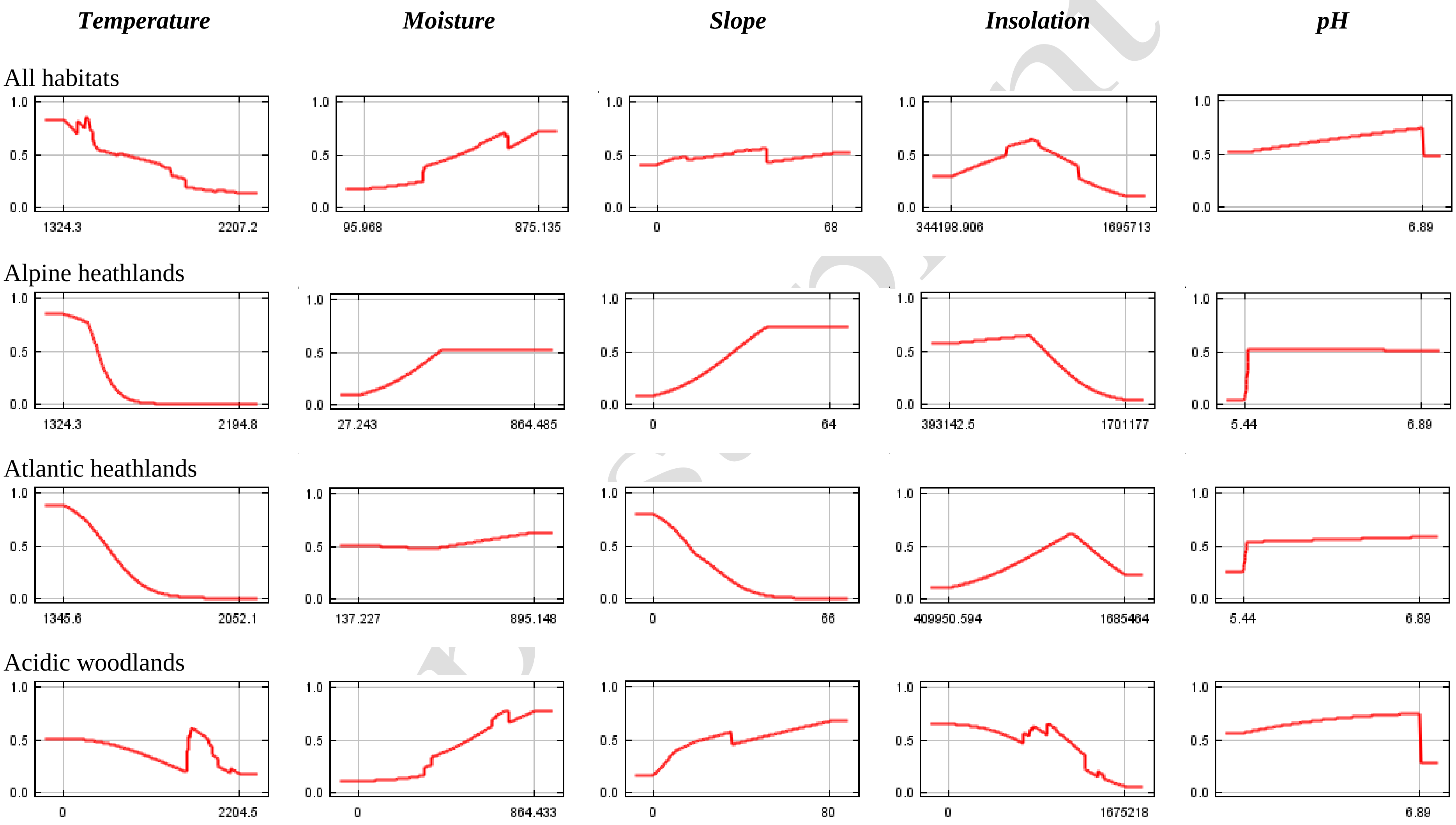
We ran a model for each type of habitat, with MaxEnt 3.3.3 (Phillips et al. 2006; Phillips and Dudik 2008), using the same background and set of predictors in all cases. The logistic outputs achieved for each habitat (shown in this annex) were used as predictors in Approach 4. Logistic outputs can be interpreted as a suitability index ranging from 0 to 1. A value near 1 represents optimal sites to hold a particular vegetation type; a value near 0 corresponds to unsuitable sites. Model predictive performance was assessed using the area under the receiver-operator characteristic curve adapted for use with presence-background samples (Phillips et al. 2006). AUC values range from 0 to 1, where 1 indicates perfect model discrimination and 0.5 a model no better than random. The achieved AUC values were: 97.5% (Alpine heathlands), 93.1% (Atlantic heathlands) and 84.0% (acidic woodlands).

Supplementary material- Annex 3. Correlation coefficients among the spatial outputs achieved for all approaches. Calculations were made on the basis of a random sample of 3000 points.



Supplementary material- Annex 4. Response curves identified by Maxent showing the effect of each predictor on the logistic response. Each curve represents a different model created using only the corresponding variable.

a) Topoclimatic variables



b) Habitat variables