

Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain)

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Animals select habitat resources at multiple spatial scales. Thus, explicit attention to scale dependency in species–habitat relationships is critical to understand the habitat suitability patterns as perceived by organisms in complex landscapes. Identification of the scales at which particular environmental variables influence habitat selection may be as important as the selection of variables themselves. In this study, we combined bivariate scaling and Maximum entropy (Maxent) modeling to investigate multiscale habitat selection of endangered brown bear (*Ursus arctos*) populations in northwest Spain. Bivariate scaling showed that the strength of apparent habitat relationships was highly sensitive to the scale at which predictor variables are evaluated. Maxent models on the optimal scale for each variable suggested that landscape composition together with human disturbances was dominant drivers of bear habitat selection, while habitat configuration and edge effects were substantially less influential. We found that explicitly optimizing the scale of habitat suitability models considerably improved single-scale modeling in terms of model performance and spatial prediction. We found that patterns of brown bear habitat suitability represent the cumulative influence of habitat selection across a broad range of scales, from local resources within habitat patches to the landscape composition at broader spatial scales.

Keywords: scale; habitat selection; habitat suitability models; Maxent, brown bear

1. Introduction

Understanding the relationships between environmental factors and species distributions is an important objective in ecology (Guisan and Zimmerman 2000) and conservation planning (Pearce and Boyce 2006). The dependence of ecological processes on drivers acting across a range of scales is a central tenet of landscape ecology (Urban 1987, Levin 1992). There are several studies that have evaluated the effect of spatial scale on the accuracy of habitat models, but very few of them have used multiple scales within the same analysis (among others, see Swindle *et al.* 1999, Dunk *et al.* 2004). When characterizing the environmental factors that influence species–habitat relationships, it is crucial to identify not only the correct drivers (Williams *et al.* 2012), but also the scale at which they match the biological interactions between organisms and the environment. Failure to address this issue can lead to a misinterpretation of the nature or strength of the pattern–process relationship (Thompson and McGarigal 2002). Thus, scaling analysis is

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particularly important for unraveling species–habitat relationships (Moudrý and Šimová 2012, Shirk *et al.* 2012, Wasserman *et al.* 2012). Species respond to habitats for particular life-history functions across a hierarchy of spatial scales (Johnson 1980, Schaefer and Messier 1995, Retie and Messier 2000). This emphasizes the importance of evaluating species habitat selection at a range of spatial scales in order to reveal the true grain at which the animals respond to the landscape (Kotliar and Wiens 1990). Recent studies focusing on different species (Thompson and McGarigal 2002, Grand *et al.* 2004, Shirk *et al.* 2010, Wasserman *et al.* 2012) have shown that species often select different habitat variables at widely divergent scales and demonstrated that multiscale approaches to habitat modeling yielded much improved predictions of species occurrence. These studies revealed the power of the bivariate scaling method of systematically varying the scale of analysis for the habitat variables to identify the dominant scales for each ecological process. Previous studies typically rely on scales suggested by expert judgment or on biological assumptions on the most meaningful single scale. There is, however, no *a priori* way to estimate the focal spatial scale at which a species perceives a particular variable (Shirk *et al.* 2012). However, ignoring the cumulative effect across multiple scales affecting the species of study may lead to reduced predictive power and to misinterpretation of relationships between environmental factors and species occurrence (e.g. Thompson and McGarigal 2002, Wasserman *et al.* 2012).

We investigated brown bear (*Ursus arctos*) habitat relationships in the Cantabrian Range (NW Spain) in an attempt to integrate the concepts of scale dependency and hierarchy of environmental factors in habitat suitability. Brown bear in northwest Spain occurs in two small, largely isolated and endangered subpopulations, with a total estimated number of individuals below 200 (Palomero *et al.* 2007). This isolation is usually attributed to increasing human pressure and to the loss of suitable habitat (Naves and Palomero 1993, Wiegand *et al.* 1998, García *et al.* 2007). The brown bear has been protected in Spain for over three decades and much of the known range of the species falls within different protected areas such as European Nature 2000 Network, Natural Parks, and the Recovery Plans of each of the Regional Institutions involved in its management. Decline of genetic diversity and the small size of the populations hamper the recovery and viability of this species (García-Garitagoitia *et al.* 2006), which is one of the most endangered mammals in Spain. Several factors make brown bear a good model for multiscale ecological analysis: (1) Brown bear home ranges are extensive; (2) The species uses a variety of resources throughout their home range; and (3) Resources for different life-history requirements (for example, foraging and mating) may require multiscale evaluations.

Brown bear ecology and habitat requirements have been broadly studied (e.g. Clevenger *et al.* 1992, 1997, Naves and Palomero 1993, Naves *et al.* 2003, Palomero *et al.* 2006) providing valuable insights into species–habitat relationships. However, few published studies consider scales issues or they do so only for factors thought to be driven at broad scales; such as population connectivity or impacts of the human footprint (Naves *et al.* 2003). We hypothesize that, as in previous studies of other species (e.g. Thompson and McGarigal 2002, Grand 2004, Wasserman *et al.* 2012), a predictive model for brown bear occurrence based on the influence of habitat variables acting at multiple optimal scales (1) would generally offer greater specificity, sensitivity, classification accuracy, and predictive power than a model constructed at a single scale and (2) may provide new and important insights into the species–habitat association that would not be apparent if scale is not explicitly optimized in habitat modeling.

Therefore, in this study we used a multiscale approach for the analysis of brown bear habitat relationships in northwest Spain. Our goals were (1) to identify the environmental drivers with a largest influence for determining brown bear habitat suitability, (2) to assess the influence of scale across a set of environmental predictors with previously demonstrated importance in habitat selection and identify the scale at which each of these variables is most important, and (3) to compare the multiscale approach to a single-scale approach and evaluate the differences relating to predictive performance and interpretation of resultant suitability maps. These results will also help to provide spatially explicit landscape-scale management recommendations for brown bear conservation planning that may benefit the persistence and potential expansion of the last remnants of this species' populations in Spain.

2. Materials and methods

2.1. Study area

The study was carried out in the Cantabrian Range (northwestern Spain), comprising the provinces of Lugo, León, Asturias, Cantabria, and Palencia (Figure 1). The study area has an extent of 49,500 km² and contains the whole known range of the brown bear in Spain, its peripheral areas, and the belt area between the two subpopulations. As shown in Figure 1, both subpopulations occupy a similar area of approximately 2500 km² each, and are separated by approximately 30 km of unoccupied range (Palomero 2007). The study region has a complex topography with altitudes ranging from sea level to 2647 m

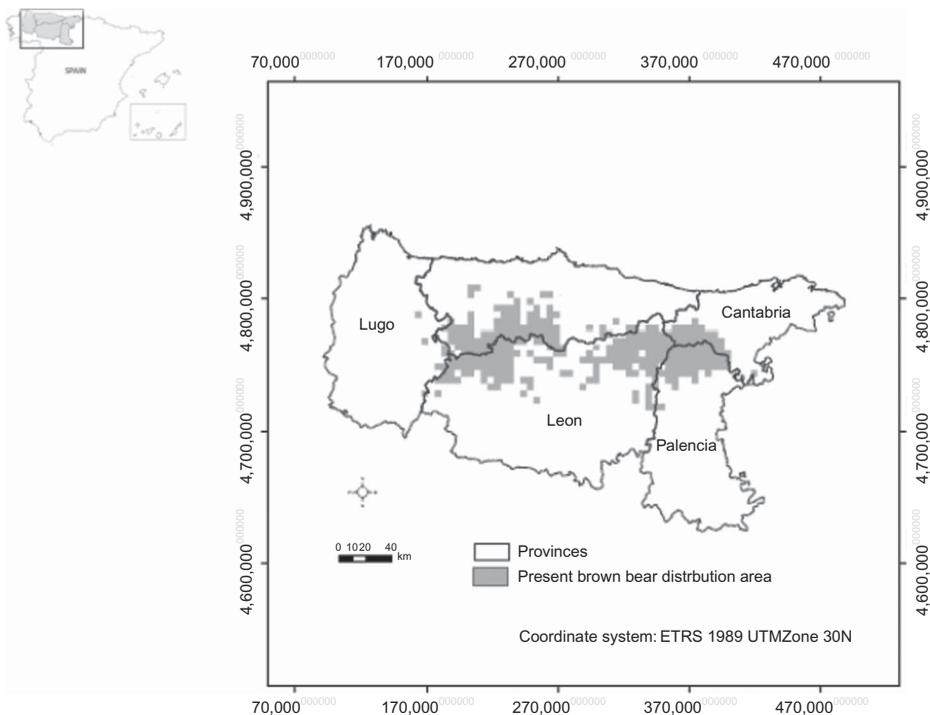


Figure 1. Study area covering the distribution range of the native brown bear populations in the Cantabrian range.

(mean elevation of 800 m), and a humid Atlantic climate with mild temperatures and short summers. According to the Third Spanish National Forest Inventory, the landscape is a mosaic of forest, shrubland, natural grasslands, and agricultural lands. Forests occupy 39% of the landscape (3.4% conifers, 11% deciduous, 17% mixed forest, and 4% plantations). The dominant native tree species are beech (*Fagus sylvatica*) and oaks (*Quercus robur*, *Quercus petraea*, and *Quercus pyrenaica*), with lesser abundance of chestnuts (*Castanea sativa*), *Pinus pinaster*, and *Pinus sylvestris*. Portions of the area have low human densities, while other portions have extensive urban and agricultural areas connected by a network of local and national roads, highways, and railways. This history of development, together with the dominant rural economic activity in the region, has led to extensive modification of the region's forest landscapes. In recent decades, tourism linked to the natural areas and mountain landscapes has gained economic importance in the Cantabrian Range.

2.2. Data

2.2.1. Species presence data

The different Regional Administrations involved in brown bear management in Spain use different types and formats of brown bear presence records collected by a number of sources, including trained observers, rangers, previous systematic studies, and local people. The data represent over 30 years of public investment and are an important source of information on brown bear occurrence patterns (direct observation, feces, and footprints). We reformatted all available location data and integrated them to create a complete presence-only database. For this study we used 8648 bear locations corresponding to the most recent records collected from 2000 to 2011.

2.2.2. Environmental data

Brown bear is a flagship species that has been extensively studied and substantial information exists on its habitat relationships. We chose to focus on variable groups previously demonstrated to have a high predictive power for brown bear occurrence (e.g. Clevenger *et al.* 1997, Naves *et al.* 2003, Apps *et al.* 2004, Posilisco *et al.* 2004, Nielsen *et al.* 2006, Kořen *et al.* 2011), including elevation, land cover–land use, and human pressure. Our candidate variable set comprised a total of 36 variables (Table 1). All variables were resampled to a UTM projection (ETRS89) with 1 ha cell size.

Elevation was obtained from the 25 m resolution digital elevation model produced in 2008 by the Spanish Geographical National Institute (CNIG). For every 1 ha cell, we calculated the mean of surrounding elevation values at six different scales using circular windows with radii 1, 2, 4, 8, 16, and 32 km. This range of radii covers the species' ecological responses to environmental gradients across all the scales relevant for meeting its daily requirements, from resources within habitat patches to the extent of reported home ranges of the species (58–1600 km²) (Huber and Roth 1993, Dahle and Swenson 2003).

We derived 11 land-cover types from information provided by the Spanish Forest Map at a scale of 1:50,000, developed within the Third Spanish National Forest Inventory (NF13). We used FRAGSTATS 3.4 (McGarigal *et al.* 2002) to calculate a number of metrics quantifying different aspects of the landscape pattern at two different levels: landscape level and class level. At the landscape level, we calculated five metrics characterizing landscape composition, configuration, and edge contrast (Table 1). At the class

Table 1. Independent variables considered for analysing brown bear habitat suitability.

Type	Metric	Description
Anthropic	HWD	Highways density
Anthropic	RD	Conventional roads density
Anthropic	RWD	Railway density
Anthropic	BD	Building density
Topographic	FM ELEV	Focal mean of elevation
Landcover	FMCC	Focal mean of canopy cover
Landcover (landscape-level metric)	CONTAG	Contagion
	CWED	Contrast-weighted edge effect
	ED	Edge density
	PD	Patch density
	SHDI	Shannon Diversity Index
Landcover (Class-level metric)	AI (1,2,3,7,10,11)	Aggregation Index
	AM_AREA (1,2,3,7,10,11)	Area-weighted mean
	COH (1,2,3,7,10,11)	Cohesion
	PLAND (1,2,3,7,10,11)	Percentage of landscape

Note: LC: landcover, (L) landscape-level metric, (CL) class-level metric. Class-level metrics were calculated for each of the following land covers: one native conifer forest, two native deciduous forest, three mixed forest, seven shrubland, 10 agricultural land, 11 non-habitat.

level, we calculated four composition and configuration metrics (Table 1) for six of the 11 cover classes that were considered to be of particular importance for the species' habitat relationships: three classes of native forest types (conifer, deciduous, and mixed); shrubland; agricultural lands (crops, cultivars, and artificial pastures); and non-habitat class (which consisted of urban and other intensive anthropic land uses). Each of these 24 metrics was calculated at the six scales mentioned above. NFI3 (Third Spanish National Forest Inventory) also provided data on canopy closure, which we used to calculate its focal mean at the six analysed scales. Indicators of human pressure, including highways, conventional roads, railways, and building vector layers, were derived at a 1:25,000 scale spatial product developed by CNIG (Spanish Geographical National Institute). We calculated the density of each of these features within focal landscapes with radii corresponding to the six analysed scales. Highways, conventional roads, and railways were assessed separately due to likely different effects depending on traffic volume and the physical restrictions of animals' movements (Kofen *et al.* 2011).

2.3. Bivariate scaling and variable pre-selection

We analysed brown bear habitat selection associated with each of the above habitat variables over the range of the six scales to identify the scale at which each independent variable was most strongly related to bear habitat suitability (e.g. Thompson and McGarigal 2002, Grand *et al.* 2004, Wasserman *et al.* 2012). We predicted relative habitat suitability based on each environmental variable at each scale using the maximum entropy algorithm Maxent (Phillips *et al.* 2006). Maxent is a general-purpose method for characterizing species habitat associations from presence-only data, and has proven to be robust and precise compared to other methods (Elith *et al.* 2006). Maxent estimates a target distribution using the known locations and a random selection of background points that maximizes entropy, subject to constraints imposed by the known occurrences. Maxent models were developed using linear and quadratic functional relations, 20,000 background data points, a maximum of

5000 iterations, and a convergence threshold of 0.00001. The regularization default settings were used (Phillips and Dudík 2008) and a random subset of 25% of the data was held out as a testing data set. To compare the performance of the models of each variable at the different scales, we used the area under the receiver operating characteristic curve (AUC, Fielding and Bell 1997), based in this case on presence versus pseudoabsence data (Phillips *et al.* 2006). In this case of very simple models, such as these single variable models, the values of AUC provided a reasonable measure of the relative importance of each environmental variable (see Golicher *et al.* 2012). For each variable we selected the scale producing the single variable model with the best performance (highest AUC value) and excluded all other scales for further analysis (e.g. Grand *et al.* 2004, Wasserman *et al.* 2012).

Once the scale selection process was completed for each independent variable, we selected a reduced number of independent variables based on a Spearman correlation coefficient clustering, correlations based on Pearson correlation coefficients, and the ecological relevance they showed in the bivariate scaling analysis. Even though, as Elith *et al.* (2011) noted, Maxent is more stable in the face of correlated variables than other algorithms, it is advisable to not include highly inter-correlated explanatory variables in any predictive modeling exercise. Accordingly, we excluded one of each variable pair that had a Pearson correlation of 0.65 or greater. This resulted in inclusion of 21 out of the 32 initial variables.

2.4. Multivariate models

To gain insights into the types of environmental factors that are more influential in determining brown bear occurrence, we developed 14 different organizational models based on habitat attributes that may be key features to bear habitat selection (e.g. Clevenger *et al.* 1997, Naves *et al.* 2003, Posilisco *et al.* 2004). These 14 organizational models correspond to the cases where brown bear habitat suitability is primarily a function of: (A) landscape composition, which informs about the amount and quality of habitat; (B) landscape configuration, depicting spatial distribution and physical connectedness of the habitat; (C) landscape edge contrast, describing the edge effects between different land-cover types; and (D) human disturbance (see Table 2 for further details). The apparent success of a model in predicting occurrence is positively related to the number of predictor variables included. Thus, within each of the 14 organizational models,

Table 2. Ecological factors used to formulate the hypotheses assessed and final variables depicting each factor.

	Ecological factors	Variables
A	Landscape composition	PLAND1, PLAND2, PLAND3, PLAND10, PLAND11, AM_AREA1, AM_AREA2, AM_AREA10, AM_AREA11, FMCC
B	Landscape configuration	COH1, COH2, COH3, COH7, AI3, AI11, FMCC
C	Edge effect	CWED
D	Human pressure	BD, HWD, RD, RWD, PLAND10, PLAND11, FMCC

Note: 14 organizational models were formulated by each of the three ecological factors alone (A, B, D) and by all the combinations among them (AB, AC, AD, ABC, ABD, ABCD, BC, BD, BCD, DC). See Table 1 for descriptions of variables.

we developed a suite of candidate hypotheses each combining subsets of five independent variables. Across the 14 organizational models, we evaluated a total of 135 alternative Maxent models, with performance assessed via the AUC statistic (see supplementary material). We formally evaluated the performance of the subset of models that had the highest AUC value using hold-out validation. For this we made 15 random partitions of the occurrence localities (75% building, 25% testing) in order to assess the average behavior of the algorithm and to allow for statistical testing of the observed differences in performance. This enabled us to evaluate the performance of the models while taking advantage of all the data.

Finally, to evaluate how scale optimization affected the predictive performance of the resultant models, we compared the best performing multiscale model (determined as described above) with the equivalent unscaled models, i.e. those built with the same independent variables but all of them measured at a single scale. We built seven unscaled models, each for one of the individual scales considered in the study (1, 2, 4, 6, 8, 16, and 32 km).

3. Results

3.1. Bivariate scaling

The bivariate scaling analysis showed substantial sensitivity of the relationship between brown bear habitat suitability and scale of analysis for all variables (see supplementary material Table s1).

The comparison among the different model scales revealed that elevation, human pressure, and landscape metrics describing diversity of land-cover classes (SHIDI) and spatial aggregation (CONTAG) were strongly related to bear habitat suitability at broad scales. A similar pattern was followed by composition metrics measuring the percentage of landscape (PLAND) in the different cover types. However, composition metrics based on the area-weighted mean patch size, in general, presented the highest AUC values at fine to medium scales. Fine-scale relationships were also seen for the canopy closure and patch cohesion of forested classes (conifers, deciduous, and mix forest) as well as for contrast-weighted edge between classes (CWED), while other metrics describing landscape fragmentation (ED and PD) showed best performance models at medium scales. Following this trend, brown bear occurrence was strongly affected by class-level configuration metrics: aggregation (AI) and patch cohesion (COH) of shrubland and anthropic land-cover classes peaked at medium to broad scales, except for aggregation of conifer forest, which expressed the strongest relationship with the species occurrence at finest scales. Further details of bivariate scaling process and particular operative scales for each predictor variable can be found in the supplementary material.

3.2. Performance of organizational models

We proposed 14 alternative organizational models, each with a number of candidate models, which represented different potential importance of landscape composition, configuration, edge, and human pressure (Table 2).

All hypotheses showed good model performance with AUC for the best models ranging from 0.836 to 0.862 (Table 3). However, differences in the performance of the various organizational models were pronounced. The best predictions of relative habitat suitability were produced using variables measuring landscape composition in combination with

Table 3. Model with best performance under each different organization models.

Organizational model	AUC MAX	VARIABLES
A	0.851	PLAND10>PLAND1>FMCC>PLAND3>PLAND2
B	0.843	COH7>AI3>COH3>COH2>COH1
D	0.842	PLAND10>HWD>BD>RD>RWD
AB	0.851	PLAND10>AI3>FMCC>PLAND1>PLAND2
AC	0.844	PLAND10>PLAND1>CWED>PLAND2>PLAND3
AD	0.862	BD>FMCC>PLAND3>PLAND2>PLAND1
ABC	0.837	FMCC>PLAND3>CWED>COH3>AI3
ACD	0.861	BD>PLAND3>FMCC>CWED>AM2
ABD	0.862	BD>COH7>FMCC>PLAND3>AM2
ABCD	0.858	BD>COH7>FMCC>PLAND3>CWED
BC	0.836	COH7>AI3>COH2>CWED>AI10
BD	0.846	COH7>BD>HWD>FMCC>AI3
BCD	0.843	COH7>BD>AI3>RD>CWED
DC	0.836	BD>HWD>FCC>RD>CWED

Note: Maximum area under the ROC curve (AUC) given by Maxent and the used variables. Variables are ordered according to their contribution to the model. See table 1 for descriptions of variables and table 2 for description of organizational models.

human pressure (AD). Organizational models combining landscape composition, configuration, and human pressure (ABD) also had a good performance. Adding human pressure to the model substantially increased model performance compared to the case when only landscape composition and configuration were considered (AB). Models combining human pressure and contrast (edge effect) (DC) showed the weakest ability to predict occurrence, together with models combining landscape configuration and contrast (BC). Adding landscape composition to the latter combination (ABC) did not increase the predictive ability, in spite of the fact that models based solely on landscape composition (A) performed relatively well. The contrast among land-cover types did not increase the performance of any combination, though its combination with landscape composition and human pressure (ACD) provides good predictive ability.

Landscape configuration (B) was a consistently weaker predictor of brown bear occurrence than landscape composition (A). In general, human disturbance presented a better performance when combined with other factors than in models comprised only by human pressure variables. Landscape composition (A) and human pressure (D) factors were included in all the hypotheses showing the best predictive ability. Also, the analysis suggested that canopy closure notably increased the performance of models containing landscape composition metrics (A) but its importance decreased in models based solely on human disturbance (D), configuration (B), contrast (C), and their combinations. Canopy closure was a covariate in all the best performing models.

Among landscape composition metrics, PLAND variables performed notably better than AREA_AM. The non-habitat cover type was not included in any high-performing model; however, agriculture showed important effects in many models. The forest cover types were very influential when used together but not so when used separately. Mixed forest generally had a higher contribution to predictive success than conifers or deciduous forests. The configuration metrics with the strongest predictive ability were patch cohesion of shrubland and aggregation of mixed forest. Finally, the most important variable measuring human disturbance was building density, followed by highway density. Conventional roads had weaker influence and railway density was the weakest human pressure predictor.

Table 4. Best performing final models.

Hypothesis ID	AUC _{1rep}	AUC _{15rep}	Std. Dev	Variables
AD_1	0.862	0.862	0.0025	BD>FMCC>PLAND3>PLAND2>PLAND1
AD_2	0.860	0.861	0.0023	BD>FMCC>PLAND3>PLAND2>AM2
AD_3	0.860	0.859	0.0041	BD>HWD>PLAND3>FMCC>PLAND2
AD_4	0.860	0.860	0.0033	BD>FMCC>PLAND3>RD>PLAND1
ABD_1	0.861	0.859	0.002	BD>COH7>FMCC>PLAND3>AM2
ABD_2	0.861	0.861	0.0021	BD>COH7>FMCC>PLAND3>AI3
ABD_3	0.860	0.859	0.0032	BD>HWD>FMCC>PLAND3>PLAND1
ACD_1	0.860	0.858	0.0021	BD>PLAND3>HWD>FMCC>CWED
ACD_2	0.861	0.860	0.0020	BD>PLAND3>FMCC>CWED>AM2

Note: The area under the ROC curve (AUC) given by Maxent when only one replication was conducted and when the average performance of the model was tested with 15 partition of the data. The variables included in each model are ordered according to their contribution. See Table 1 for description of variables and Table 2 for description of organizational models

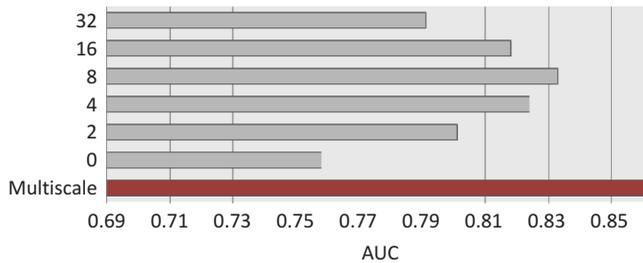


Figure 2. Performance of the scaled and unscaled models. The plot shows the Area Under the Roc Curve (AUC) for multiscale model AD1 (see Figure 3) and for the single-scale models with all the variables computed at a given scale (1, 2, 4, 8, 16, and 32 km).

The nine top-performing models all had AUC values between 0.860 and 0.862. Four of them were formulated under organizational model AD, whereas the others were distributed on hypotheses ABD (three models) and ADC (two models). Executing multiple runs of these models with 15 random partitions enabled us to test model performance and variability, and allowed us to select those with best predictive success (Table 4). Four of the nine models that showed the highest average AUC were selected for further evaluation: AD (two models), ABD (one model) and ACD (one model). The final models showed very slight differences in their performance under cross-validation (Figure 2) and their predicted ecological suitability maps were similar (Table 5). They all included the variables building density and focal mean of canopy closure and composition metrics for several forest types, except the one under the ABD organizational model, which contained information about composition and configuration of mixed forest and shrubland.

There were substantial differences in predictive performance between the scaled and unscaled models (Figure 3). The scaled model showed remarkably higher discrimination ability (as measured by AUC) than the unscaled models. Models developed with all variables measured at the finest scale (1 km) showed the weakest performance (AUC = 0.758), while the highest AUC for the single-scale models was obtained at 8 km (AUC = 0.833). There were also considerable differences in the patterns of habitat suitability across the study area between the best scaled and unscaled models (Figure 4). The correlation in the

spatial predictions of scaled and unscaled models was 0.41 and 0.73 when comparing the multiscale model with the single-scale model measured at 1 km and 8 km, respectively.

4. Discussion

4.1. Determinants of brown bear habitat suitability

Our results indicated that landscape composition together with human disturbance were dominant drivers of bear relative habitat suitability, highlighting the importance of landscapes with large extents of undisturbed forest and low human footprint. Human disturbance improved the discriminatory power of all models in which it was included. Agricultural lands showed a strong relationship with bear habitat suitability, suggesting a marked avoidance of anthropic cover types at broad spatial scales. The density of buildings was the most influential variable in the group, indicating that brown bears avoid areas in the landscape up to a considerable distance (16 km) away from human settlements.

Table 5. Correlation between final models.

	AD_1	AD_2	ABD_2	ACD_2
AD_1	1	0.992	0.954	0.959
AD_2		1	0.945	0.96
ABD_2			1	0.969
ACD_2				1

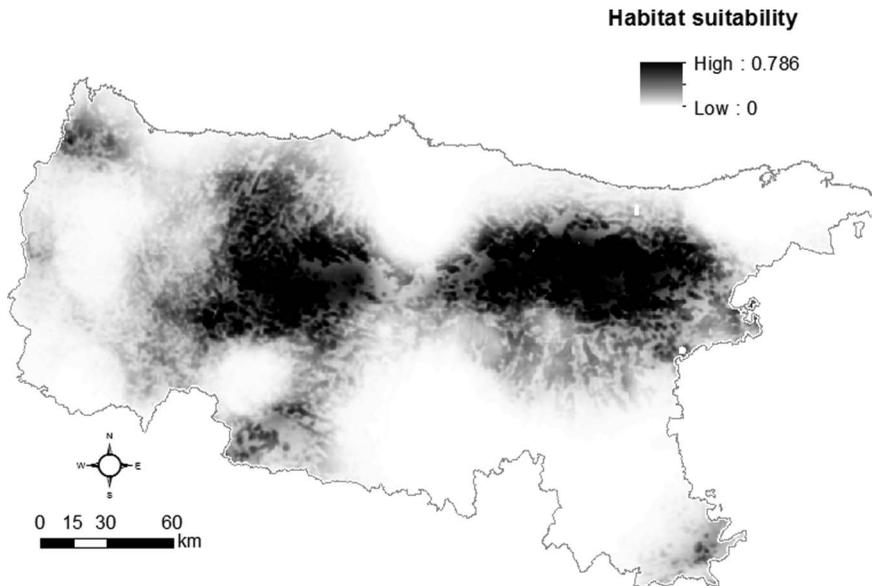


Figure 3. Habitat suitability map provided by optimized multiscale model AD1. The variables in this model are building density (BD, scale 16 km); Canopy closure (FMCC, scale 1 km); percentage of the landscape covered by mixed forest (PLAND3, scale 32 km); percentage of the landscape covered by deciduous forest (PLAND2, scale 8 km); and percentage of the landscape covered by conifer forest (PLAND1, scale 32 km). Darker colors identify the areas with highest probability of brown bear occurrence. Only one of the four top predictive models is represented (AD1) due to high similarities in the output suitability maps.

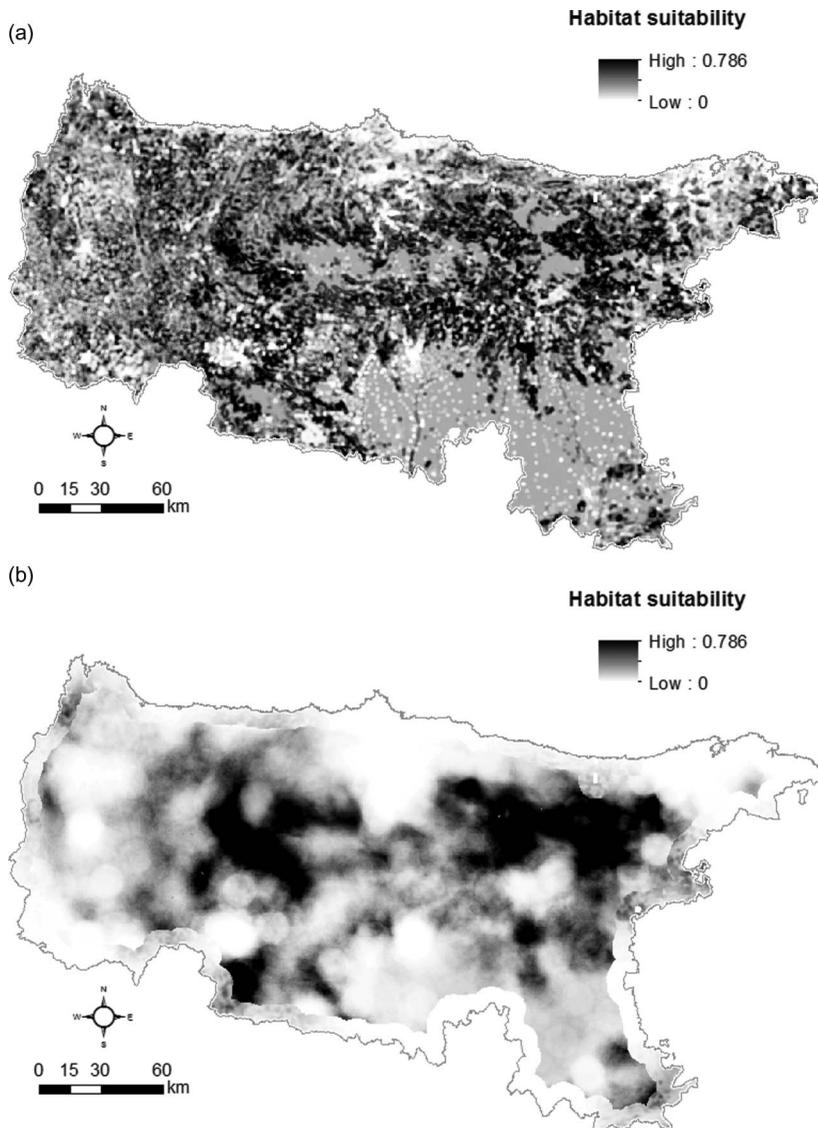


Figure 4. Suitability map provided by the unscaled models, i.e. those built with all the independent variables calculated at the same scale of 1 km (a) and 8 km (b). B is the single-scale model with the highest AUC while A corresponds to a local scale at which habitat relationships for the brown bear have been frequently assessed in previous studies.

Interestingly, highways provided a less predictive ability, while roads and railways had a much lower effect on model performance. This suggests that bear relative habitat suitability is highly related to human population density and activities in the landscape, but less related to proximity to transportation infrastructure (particularly those with relatively low traffic volume).

The results also clearly showed that landscape configuration, including patch size, aggregation, and edge density, had relatively weak relationships with brown bear relative habitat suitability in Spain, and was much less important than landscape composition. This

is in agreement with the general pattern of habitat extent being more important than habitat configuration in most instances (Cushman and McGarigal 2002, Fahrig 2003). Many studies have found that habitat availability is more important than habitat configuration in predicting the occurrence or relative abundance of species in fragmented landscapes (Martensen *et al.* 2008, Boscolo and Meztger 2011, Awade *et al.* 2012). This is also consistent with ecological knowledge of the species: brown bear has high dependence on forest cover, suggesting that landscape composition should dominate its habitat relationships (Clevenger *et al.* 1992). The comparatively weak role of landscape configuration may also be related to the high mobility of the species, which allows it to integrate across landscapes of differing configurations such that a fragmented patch mosaic may not function as poorly connected habitat for this species, so long as the fragmentation is not by landscape elements avoided at broad scales, such as human settlements, or by impermeable barriers to movement.

Within the configuration variables, patch cohesion of shrubland was more influential than patch cohesion of forest types. This may suggest that shrubland may provide complementary (or even supplementary) foraging resources as well as linkage areas through which bears can move between other habitat patches. Thus the spatial connectedness of shrublands may be important in terms of shelter, matrix permeability, and habitat continuity.

The amount of available habitat had a stronger relationship with bear occurrence when measured as percentage of landscape area of all three forest types combined. This suggests that the three forest types are similarly important for brown bears in the Cantabrian range, either because the bears do not specialize or discriminate between forest types when selecting suitable habitat, or because the combination of the resources available in different forest types is particularly beneficial for the species. Previous research has suggested that conifer forests in Spain are of lower quality as habitat for brown bear than are deciduous forests (Clevenger *et al.* 1997). Though positive influence may be found in the selection of deciduous and mixed forests that contain abundant food (Clevenger *et al.* 1997), conifers may provide other important life requisites such as thermal regulation and security (Blanchard 1983; McLean and Pelton 1990; Apps *et al.* 2004).

Canopy cover added predictive power to all models that included landscape composition variables. This further supports our contention that the extent of forest cover is a major component of habitat quality for this species. This is supported by the fact that this variable was included in all of the nine best performing models.

4.2. Scale dependence of habitat selection

Brown bear habitat selection appeared to be driven by habitat factors at multiple scales. The predictive ability of the variables changed notably depending on the scale at which they were measured. Across independent variables, all six scales were selected as the most predictive. Bears appeared to respond more strongly to indicators of human disturbance, such as building density, transportation infrastructure, and agriculture at medium to broad scales. This suggests that bears perceive human disturbance at large scales and thus these features have large- and broad-scale cumulative effects on habitat suitability. Elevation also showed a broad-scale dominant pattern, which may be related to the same large distance avoidance of human activities by brown bear, due to the association between less human footprint and higher elevation areas.

Our results when related to landscape configuration present an interesting contrast to those reported by Naves *et al.* (2003), who found that forest connectivity was a better

predictor at a broader scale than shrubland connectivity. In contrast, we found that forest configuration metrics had better performance when measured at finer scales than shrubland. This difference is most likely due to the higher resolution of our scaling analysis. That previous study used a broader grain of 25 km² and considered multiple spatial scales by introducing connectivity of forest and shrubland to describe large-scale properties of these variables. At a coarser grain the scale considered to measure forest connectivity (two-cell focal area) was broader than the one used to measure shrubland connectivity (one cell focal area).

The influence of the edge effect among cover types and of canopy closure was highest at the finest scales. This fine-scale sensitivity to edge contrast and canopy closure probably reflects a tendency of brown bear to associate with edges and ecotones for supplementary and complementary resource use. Clevenger *et al.* (1997) showed that brown bears selected shrubby grasslands and ecotones between woodland and grassland or cultivated areas where they could obtain a juxtaposition of foraging and cover.

4.3. Performance and spatial patterns of scaled and unscaled habitat suitability models

The high variability among the predictor variables as to the scale at which they most strongly predicted bear relative habitat suitability was notable, which may have large implications for interpreting brown bear habitat relationships. In addition to large differences in model performance, the relative habitat suitability of the species across the study area was substantially different between the scaled and unscaled models.

In particular, the model relying on local scales (1 km) resulted in dramatically different ecological interpretation and mapping of habitat compared to the best performing multi-scale model (see Figures 2 and 4a). It is important to note that most previous research on the habitat use of this species employed single-scale analysis, often using 1 km extents (e.g. Nielsen *et al.* 2006, García *et al.* 2007, Kořen *et al.* 2011). While the multiscale model output map markedly showed the two population core habitat areas to be associated with the current species range, the local single-scale model (1 km) (Figure 4a) failed to clearly discriminate these cores. The 1 km unscaled model overpredicted the probability of brown bear on less optimal habitat, whereas it underpredicted the probability of occurrence in areas currently occupied by brown bear. The correlation of spatial predictions of both models showed that the predicted relative habitat suitability values are markedly different. The same pattern of weaker relationships and overprediction of quality in suboptimal habitat and underprediction of quality habitat has been reported in other scale optimization habitat modeling studies (e.g. Shirk *et al.* 2012, Wasserman *et al.* 2012). The possible solution of broadening the scale of the single-scale model was not fully satisfactory, and a number of drawbacks were also found. Focusing on the best single-scale model (8 km) showed that, though an improvement in predictive performance was achieved, fine-scale factors that are also significant in the species' use of habitat were disregarded (Figure 4b). This resulted in a habitat model whose pattern was an oversimplification of the more detailed mapping provided by the multiscale model. This model's ecological spatial predictions gained similarity with the multiscale one but still relative habitat suitability values were different and may lead to distinct interpretations of the species habitat suitability. The omission of such fine-scale factors in the unscaled model at 8 km can have a large impact on the actual ability of the model to guide multiple-scale forest management and conservation plans (from the stand to the landscape level) to promote species persistence and potential population expansion. The suitable habitat identification was achieved in the multiscale

model without excessive aggregation, retaining and making possible to appreciate local details and variations that may be blurred or completely lost at broader single-scale models (Figure 4b). In this way, both large-scale and fine-scale factors that together determine brown bear perception and use of habitat could be accounted for in the final models, providing clear evidence for the multiscale nature of brown bear habitat selection in Spain.

5. Conclusions

The scaled model suggests that relative habitat suitability for the brown bear is highly associated with landscapes with large extents of forests intermixed with shrublands, and with a low density of human settlements. Although these optimal areas are of limited extent and are concentrated around the area currently occupied by the two subpopulations, the habitat suitability map also shows other sectors where additional high relative habitat suitability exists that could be the focus of conservation and restoration efforts. This will be valuable to support the identification and prioritization of areas where bears can meet their ecological needs and that are more likely to accommodate or promote the species range expansion. The models presented in this article provide the basis for further analysis about linkages among habitat patches to guide management to enhance connectivity between the two main isolated subpopulations of brown bear in the northwest of Spain, and therefore to ensure the long-term viability and conservation of this endangered species.

Our findings strengthen the perspective that identifying an optimal or adequate scale of each predictor is a key issue when inferring brown bear habitat relationships. Even when the appropriate predictors are selected, an incorrect specification of the scale at which they operate could lead to incorrect conclusions about the species habitat suitability and therefore lead to improper management recommendations. The unscaled models were much weaker, less discriminant, and provided substantially different predictions, which would lead to drastically different interpretation of which factors (and related management measures) are important for brown bear habitat relationships as well as the spatial scales at which these factors influence brown bear.

Very few habitat studies have formally assessed the scale relationships between each predictor variable and habitat suitability. Scale dependency in habitat modeling has only recently been a focus of research, and most studies that have considered scale have evaluated a series of models in which all variables were at the same scale, which differed between models. Our analyses and similar work on other species (e.g. Thompson and McGarigal 2002, Shirk *et al.* 2012, Wasserman *et al.* 2012) suggests that independently optimizing the scale of analysis of each predictor variable may be crucial to obtain reliable predictions of species distribution and habitat. This supports the knowledge that an organism's location is not necessarily influenced by the effects of habitat at any one single scale (Wasserman *et al.* 2012). Different species scale the environment differently, and within a given species different habitat factors are selected at different scales simultaneously (e.g. Shrik *et al.* 2012). Since no evident patterns for dominant scales across the different groups of variables were identified in this study, we recommend an optimization process to select an optimal scale of each predictor coupled with different organizational models of the importance of different kinds of ecological drivers (such as landscape composition, configuration, edge effects, and human disturbance).

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References

- Apps, C.D., *et al.*, 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*, 68, 138–152.
- Awade, M., Boscolo, D., and Metzger, J.P., 2012. Using binary and probabilistic habitat availability indices derived from graph theory to model bird occurrence in fragmented forest. *Landscape Ecology*, 27, 185–198.
- Blanchard, B.M., 1983. Grizzly bear: habitat relationships in the yellowstone area. *International Conference on bears Research and Management*, 5, 118–123.
- Boscolo, D. and Metzger, J.P., 2011. Isolation determines patterns of species presence in highly fragmented landscapes. *Ecography*, 34, 1018–1029.
- Clevenger, A.P., Purroy, F.J., and Campos, M.A., 1997. Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. *Biological Conservation*, 80, 17–22.
- Clevenger, A., Purroy, F., and Pelton, M., 1992. Brown bear (*Ursus arctos* L.) habitat use in the Cantabrian Mountains, Spain. *Mammalia*, 56, 203–214.
- Cushman, S.A. and McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology*, 17, 637–646.
- Dahle, B. and Swenson, J.E., 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, 260, 329–335.
- Dunk, J.R., *et al.*, 2004. Predicting the occurrence of rare mollusks in northern California forests. *Ecological Applications*, 14, 713–729.
- Elith, J., *et al.*, 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.
- Elith, J., *et al.*, 2011. A statistical explanation of Maxent for ecologists. *Diversity and Distributions*, 17, 43–57.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.
- Fielding, A.H. and Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38–49.
- García, P., *et al.*, 2007. Detailed model of shelter areas for the Cantabrian brown bear. *Ecological Informatics*, 2, 297–307.
- García-Garitaigoitia, J.L., Rey, I., and Doadrio, I., 2006. Variabilidad genética. In: G. Palomero, F. Ballesteros, J. Herrero, and C. Nores, eds. Demografía, distribución, genética y conservación del oso pardo cantábrico. Madrid: Parques Nacionales, 71–90.
- Golicher, D., *et al.*, 2012. Pseudo-absences, pseudo-models and pseudo-niches: pitfalls of model selection based on the area under the curve. *International Journal of Geographical Information Systems*, 26, 2049–2063).
- Grand, J., *et al.*, 2004. A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine–scrub oak community. *Conservation Biology*, 18, 1063–1077.
- Guisan, A. and Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147–186.
- Huber, D. and Roth, H.U., 1993. Movements of European brown bear in Croatia. *Acta Theriologica*, 38, 151–169.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.
- Koreň, M., *et al.*, 2011. Habitat suitability modelling from non-point data: the case study of brown bear habitat in Slovakia. *Ecological Informatics*, 6, 296–302.
- Kotliar, N.B. and Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, 59, 253–260.
- Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, 73, 1943–1967.
- Martensen, A.C., Pimentel, R.G., and Metzger, J.P., 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: implications for conservation. *Biological Conservation*, 141, 2184–2192.

- McGarigal, K., et al., 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available from: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McLean, P.K. and Pelton, M.R., 1990. Relationships between industrial activity and grizzly bears. *International Conference on Bears Research and Management*, 8, 105–112.
- Moudrý, V. and Šimová, P., 2012. Influence of positional accuracy, sample size and scale on modelling species distributions: a review. *International Journal of Geographical Information Systems*, 26, 2083–2095.
- Naves, J., et al., 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conservation Biology*, 17, 1276–1289.
- Naves, J. and Palomero, G., eds., 1993. *El oso pardo (Ursus arctos) en España. Colección Técnica, Instituto Nacional para la Conservación de la Naturaleza*, Madrid: ICONA.
- Nielsen, S.E., Stenhouse, G.B., and Boyce, M.S., 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, 130, 217–229.
- Palomero, G., et al., 2007. Trends in number and distribution of brown bear females with cubs-of-the-year in the Cantabrian Mountains, Spain. *Ursus*, 18, 145–157.
- Palomero, G., et al., eds., 2006. *Demografía, distribución, genética y conservación del oso pardo cantábrico*. Madrid: Parques Nacionales.
- Pearce, J.L. and Boyce, M.S., 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, 43, 405–412.
- Phillips, S.J., Anderson, R.P., and Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259.
- Phillips, S.J. and Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161–175.
- Posillico, M., et al., 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. *Biological Conservation*, 118, 141–150.
- Rettie, W.J. and Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, 23, 466–478.
- Schaefer, J.A. and Messier, F., 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography*, 18, 333–344.
- Shirk, A., et al., 2010. Inferring landscape effects on gene flow: a new model selection framework. *Molecular Ecology*, 19, 3603–3619.
- Shirk, A.J., et al., 2012. *Scale dependency of American marten (Martes americana) habitat relationships. Biology and conservation of martens, sables, and fishers: a new synthesis*. Ithaca, NY: Cornell University Press.
- Swindle, K.A., et al., 1999. Old-forest distribution around spotted owl nests in the central Cascade Mountains, Oregon. *Journal of Wildlife Management*, 63, 1212–1221.
- Thompson, C.M. and McGarigal, K., 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). *Landscape Ecology*, 17, 569–586.
- Urban, D.L., 1987. Landscape ecology. *Bioscience*, 37, 119–127.
- Wasserman, T.N., et al., 2012. *Multi scale habitat relationships of Martes americana in northern Idaho, U.S.A. Res. Pap. RMRS-RP-94*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 21p.
- Wiegand, T., et al., 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs*, 68, 539–570.
- Williams, K.J., et al., 2012. Which environmental variables should I use in my biodiversity model? *International Journal of Geographical Information Systems*, 26, 2009–2047.