

*Seasonal and temporal changes in species use of the landscape: how do they impact the inferences from multi-scale habitat modeling?*

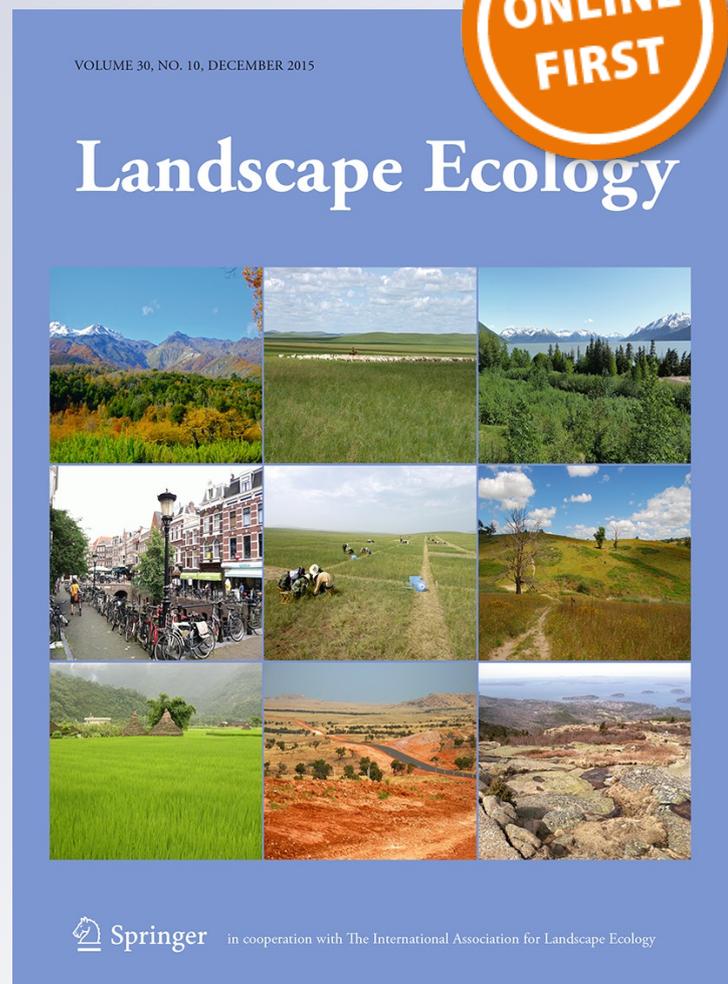
**María C. Mateo-Sánchez, Aitor Gastón, Carlos Ciudad, Juan I. García-Viñas, Jorge Cuevas, César López-Leiva, Alfredo Fernández-Landa, et al.**

**Landscape Ecology**

ISSN 0921-2973

Landscape Ecol

DOI 10.1007/s10980-015-0324-z



**Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media Dordrecht. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Seasonal and temporal changes in species use of the landscape: how do they impact the inferences from multi-scale habitat modeling?

María C. Mateo-Sánchez · Aitor Gastón · Carlos Ciudad ·  
Juan I. García-Viñas · Jorge Cuevas · César López-Leiva ·  
Alfredo Fernández-Landa · Nur Algeet-Abarquero · Miguel Marchamalo ·  
Marie-Josée Fortin · Santiago Saura

Received: 14 May 2015 / Accepted: 8 December 2015  
© Springer Science+Business Media Dordrecht 2015

## Abstract

**Context** Multi-scale approaches to habitat modeling have been shown to provide more accurate understanding and predictions of species-habitat associations. It remains however unexplored how spatial and temporal variations in habitat use may affect multi-scale habitat modeling.

**Objectives** We aimed at assessing how seasonal and temporal differences in species habitat use and distribution impact operational scales, variable influence, habitat suitability spatial patterns, and performance of multi-scale models.

**Methods** We evaluated the environmental factors driving brown bear habitat relationships in the Cantabrian Range (Spain) based on species presence records (ground observations) for the period 2000–2010,

LiDAR data on forest structure, and seasonal estimates of foraging resources. We separately developed multi-scale habitat models for (i) each season (spring, summer, fall and winter) (ii) two sub-periods with different population status: 2000–2004 (with brown bear distribution restricted to the main population nuclei) and 2005–2010 (with expanding bear population and range); and (iii) the entire 2000–2010 period.

**Results** Scales of effect remained considerably stable across seasonal and temporal variations, but not the influence of certain environmental variables. The predictive ability of multi-scale models was lower in the seasons or periods in which populations used larger areas and a broader variety of environmental conditions. Seasonal estimates of foraging resources, together with LiDAR data, appeared to improve the performance of multi-scale habitat models.

**Conclusions** We highlight that the understanding of multi-scale behavioral responses of species to spatial

---

Special issue: Multi-scale habitat modeling.

---

Guest Editors: K. McGarigal and S. A. Cushman.

---

M. C. Mateo-Sánchez (✉) · A. Gastón ·  
C. Ciudad · J. I. García-Viñas · J. Cuevas ·  
C. López-Leiva · S. Saura  
ECOGESFOR Research Group, E.T.S.I Montes, Forestal  
y del Medio Natural, Technical University of Madrid,  
Ciudad Universitaria s/n, 28040 Madrid, Spain  
e-mail: mc.mateo@upm.es

A. Fernández-Landa  
Agresta Cooperative Society, C/Duque Fernán Núñez 2,  
28012 Madrid, Spain

N. Algeet-Abarquero · M. Marchamalo  
Department of Land Morphology and Engineering,  
Technical University of Madrid, ETSI Caminos, Canales  
y Puertos, c/Profesor Aranguren s/n, 28040 Madrid, Spain

M.-J. Fortin  
Department of Ecology and Evolutionary Biology,  
University of Toronto, 25 Harbord Street, Toronto,  
ON M5S 3G5, Canada

patterns that continually shift over time may be essential to unravel habitat relationships and produce reliable estimates of species distributions.

**Keywords** Multi-scale habitat modeling · Operational scale · Habitat seasonality · Foraging resource · Population size · Brown bear

## Introduction

The sensitive dependence of ecological processes to drivers acting across a range of scales has been constantly revisited from the most theoretical perspectives of landscape ecology (Urban 1987; Levin 1992) to the most practical and recent ecological modeling (Vicente et al. 2014). There is a consensus in literature that species respond to habitat at different scales (Johnson 1980; Schaefer and Messier 1995; Rettie and Messier 2000; Grand et al. 2004; Fortin et al. 2012), yet many studies have usually considered this response only at a single spatial scale (e.g. Holland and Fahrig 2000; Triantis et al. 2003; Posillico et al. 2004). Spatial scale may refer to the grain size at which the environmental variables are mapped, to the spatial extent at which the effect of the environmental variable is quantified around a given location (typically through a mean value of the variable over the considered spatial extent), or to a combination of both.

When characterizing species-habitat relationships, it is critical not only to identify the correct drivers but also the scale (spatial extent) at which they have their strongest effect (hereafter referred as operational scale). Recent studies (e.g. Grand et al. 2004; Holland et al. 2004; Shirk et al. 2012; Wasserman et al. 2012; Weaver et al. 2012; Mateo-Sánchez et al. 2014) have supported this point and demonstrated that multi-scale approaches to habitat modeling yield improved predictions of species occurrence. Multi-scale habitat modeling may capture dimensions that have been ignored by usual approaches conducted at single scale (Pearson et al. 2004). Failure to address the variability of species responses with scale can strongly affect inferred habitat relationships and lead to a misinterpretation of interactions between species and the environment with potentially large conservation implications (Bradley et al. 2010; Shirk et al. 2012).

Several authors have emphasized the importance of analytical processes aimed to select the operational

scale for each predictor when modeling habitat selection (Kotliar and Wiens 1990; Holland et al. 2004; Wasserman et al. 2012). One advocated method to estimate the spatial scale at which a species perceives a particular landscape variable is to model the species-habitat relationship at a number of scales and determine which scale fits the model best (Savignac et al. 2000; Wasserman et al. 2012; Mateo-Sánchez et al. 2014). However, multi-scale habitat models so far have mainly focused on a single period of time with a particular distribution of individuals given by the presence data that usually feed these models. Some authors have suggested that operational scales may be influenced by species traits such as space use (i.e., home ranges in mammals; see Jackson and Fahrig 2012) or perceptual abilities (Zollner 2000). There are evidences that the species space use can vary in relation to seasonal variation in food availability (Anderson et al. 2005), breeding (Pope et al. 2000), population size and status (i.e., growing or decreasing population; McFarland et al. 2014) or other factors (Kie et al. 2002; Anderson et al. 2005). However, it remains yet unexplored how seasonal or temporal changes in species distributions may affect the operational scales, inferences and habitat suitability patterns of multi-scale habitat modeling.

Our aim in this study was to address this gap in knowledge by assessing the potential impact of seasonal and temporal changes on multi-scale model performance and on the ecological understanding of multi-scale species responses and distribution drivers. We focus on the effect of scale defined as the spatial extent at which the measured environmental variables are perceived by species, while keeping the grain size constant. We investigate brown bear (*Ursus arctos*) habitat relationships in the Cantabrian Range (NW Spain) as the focal species for this study for different reasons. First, brown bear is one of the most endangered mammals in Spain. Even when recent studies (Ballesteros and Palomero 2012) reveal that the population is growing, limited habitat availability has been identified as one of the major conservation concerns and potential constraints for the long-term persistence of this species. Second, brown bear has, as other large mammals, broad spatial requirements with variable pattern of space use due to seasonality (Börger et al. 2006), which, together with the recent population expansion in the Cantabrian Range, makes this species a good model organism for the objectives

of this study. Third, brown bear in the Cantabrian Range counts with a large long-term occurrence data set and its habitat requirements have been broadly studied (e.g. Clevenger et al. 1992; Naves and Palomero 1993; Naves et al. 2003; Mateo-Sánchez et al. 2014), providing valuable support on understanding species-habitat relationship. Furthermore, we were able to estimate, based on LiDAR data, forest shelter as well as seasonal foraging resources for brown bears over the  $\approx 35,700 \text{ km}^2$  study area. All these factors offer a unique opportunity to assess the variability of the scale (spatial extent) of habitat relationships along temporal and spatial processes, and to test how multi-scale habitat models predictions change over the seasons and different time periods.

We addressed our general objective through two specific analyses. First, we separately considered the seasonal (spring, summer, fall and winter) brown bear presence records and foraging resources for the period 2000–2010, in order to gain insights on how seasonal habitat use may affect the operational scales that are identified through multi-scale habitat modeling as well as the predictions of species occurrence. Then, we investigated how two different multi-annual periods (2000–2004 vs. 2005–2010), with distinctive population size and status, may affect the extents at which individuals perceive and use the landscape and the ability of multi-scale models to predict species occurrence. In both cases, the results of these analyses were compared to those of a conventional (year-round) multi-scale habitat model for the entire period 2000–2010.

## Methods

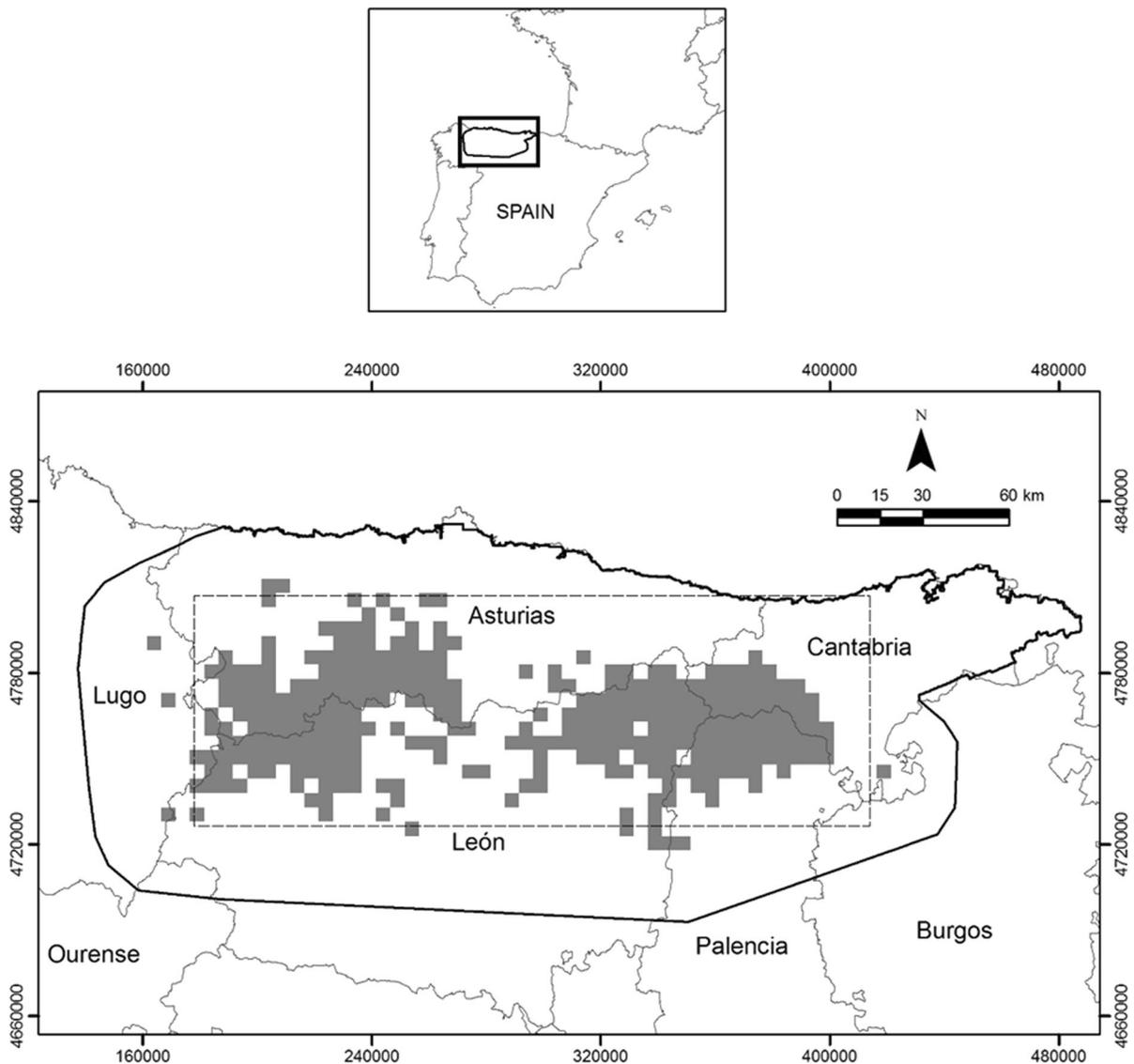
### Study area

The study was carried out in a  $\approx 35,700 \text{ km}^2$  area located in the Cantabrian Range (NW Spain,  $42^\circ 51' \text{N}$ ,  $5^\circ 34' \text{W}$ ) (Fig. 1). This area comprises the whole known range of the brown bear native populations in the Iberian Peninsula, and its peripheral zones where future population expansion may be likely (buffer of  $\sim 25 \text{ km}$  around current species range). The study region has a complex topography (elevations ranging from sea level to 2648 m) and a humid Atlantic climate with mild temperatures and short summers. According to the forest map of Spain (FMS) the

landscape is composed by a mosaic of forests (39 %), shrublands (24 %), natural grasslands (3 %), rocky areas (2 %), croplands (22 %) and other artificial or highly modified areas (10 %). Forests are dominated by deciduous oaks (*Quercus robur* and *Q. petraea*), beeches (*Fagus sylvatica*) and chestnuts (*Castanea sativa*) mainly in northward slopes of the range. Extensive forests of semi-deciduous oaks (*Q. pyrenaica* and *Q. faginea*) and also evergreen oaks (*Q. ilex*) are found on southern slopes. *Pinus* sp. and *Eucalyptus globulus* are also relatively abundant in the area. A large variety of shrubland species is found in the Cantabrian Range (*Erica* sp., *Calluna vulgaris*, *Vaccinium myrtillus*, *Crataegus* sp., *Rubus* sp., *Prunus spinosa*, *Rosa* sp., *Cytisus* sp., *Genista* sp., *Ulex* sp., *Rhamnus alpina*, etc.). Some parts of the study area have low human population density, whereas others have experienced extensive urban and agriculture development connected by a network of transport infrastructures. As a result of the extensive and long-lasting anthropogenic activities in this region, the original forest landscape has suffered significant modifications.

### Species presence data

We used available brown bear presence records for the period 2000–2010 collected in the Cantabrian Range by trained observers and rangers. Presence records were obtained through direct observation and indirect evidence (feces, footprints, hair, beehives attacks); the diversity of presence data sources might allow a comprehensive representation of brown bear occurrence patterns, particularly given that the same type of records is used for comparing the different seasons and time periods. We reformatted all these occurrence data and integrated them to create a complete presence-only dataset. Locations were resampled with 1 ha cell size to summarize potential locations of the same individual in consecutive days and to allow computational efficiency. This is the same cell size used in previous studies for this species (Mateo-Sánchez et al. 2014). We obtained a total number of 6207 locations for the entire period 2000–2010 that were used in subsequent analyses. The same procedure was followed to obtain bear locations separately for each season: spring (2034 locations), summer (2226 locations), fall (1316 locations) and winter (844 locations). We considered a non-hibernation hypothesis for



**Fig. 1** Location of the study area and brown bear range (*gray squares*) in the Cantabrian Range. *Dashed rectangle* indicates a focused area shown in Figs. 2 and 3. The names of the Spanish provinces are indicated

winter since there are evidences that in the Cantabrian Range bears reduce only partially, and not completely, their activity in winter (Palomero 1995; Naves et al. 2001; Palomero et al. 2011). To assess the effects of temporal changes in population size on habitat use, we subdivided and summarized, following the same procedure, the bear locations in two multi-annual periods: a “constrained” period (2000–2004, 1746 locations) with a smaller population size of about 80 individuals (Wiegand et al. 1998; Naves et al. 1999) and a “growth” period (2005–2010, 4744 locations)

with a noticeable population increase up to about 200 individuals in 2011 (Ballesteros and Palomero 2012), i.e. more than doubling the previously estimated population size.

Overview of environmental data and assessed scales

We used environmental variables related to foraging resources, shelter and human pressure that have shown to be suitable predictors of brown bear occurrence

(Clevenger et al. 1997; Naves et al. 2003; García et al. 2007; Koreň et al. 2011; Mateo-Sánchez et al. 2014). A set of 12 variables (Table 1) was referenced to a UTM projection (ETRS89, zone 30) and resampled with 1 ha cell size. To generate raster layers for multiple spatial extents, we used circular moving windows around each location with radii 0.25, 0.5, 1, 2, 4, 8, 16, 32 and 64 km as the scales for each variable (see Mateo-Sánchez et al. 2014 for details). This range of radii covers the species responses to environmental gradients across all the scales (i.e. extents) relevant for meeting its ecological requirements, from resources within habitat patches to the extent of home ranges and broader landscape-scale impacts. We used ArcGIS 10.1 (ESRI) for calculations.

#### LiDAR data

LiDAR information was provided by the Spanish National Plan for Aerial Orthophotography (PNOA; Ministerio de Fomento 2015) with a mean density of 0.5 points per m<sup>2</sup> and vertical root mean square error (RMSE)  $\leq 0.15$  m. A total of 10,544 tiles (2 × 2 km), weighting 1.3 Tb, were processed with FUSION software (McGaughey and Carson 2003). A predefined height of 3.5 m was used as the threshold to separate trees from understory vegetation. Forest height was estimated as the 95th percentile of vegetation height from the aboveground vegetation returns ( $>3.5$  m from the ground), i.e. of laser pulses intercepting vegetation and returning to the sensor. Forest canopy cover was computed as the ratio between the number of first returns above 3.5 m and the total number of first returns (a laser pulse may intercept several vegetation targets from the top of the tree to branches or understory vegetation; only the first return was considered).

#### Foraging resources

Foraging resources for brown bears in each 1 ha cell were estimated for each particular season from LiDAR data, the FMS at a 1:50,000 scale (developed in coordination with the Third Spanish National Forest Inventory), and specific plant species abundance models (Table 1). We estimated foraging resources from the combination of those plant species (trees, shrubs and herbs) which sequentially provide food supply for brown bears along the different seasons

(Marquínez 2002; Palomero et al. 2011). Main forage resources comprise herbaceous plants in spring (mostly hydrophyllous tall herbs). Fleshy fruits and berries largely provided by shrublands (species such as *V. myrtillus*, *Crataegus* sp., *Rubus* sp., *P. spinosa* and *R. alpine*) seem to be especially important for bears. In fall and winter acorns, beech nuts and chestnuts are the fundamental component of brown bear diet. The abundance and importance of the resources provided by each plant species were both accounted for, as in Nielsen et al. (2010). The importance of each foraging resource was determined by previous seasonal scat-analysis for brown bears in the study area (Delibes 1999; Fernandez-Calvo et al. 2001; Marquínez 2002; Ballesteros et al. 2012). The abundance of tree species was obtained from FMS (species identity and occupied area in a given map polygon) and LiDAR data (canopy cover within the occupied area). The abundance of non-tree species was estimated through the information in available floristic inventories, ecological niche modeling (penalized logistic regression) based on previously available species distribution models that predict occurrence probability in each cell of the study area for each shrub species using climate and lithology (Gastón and García-Viñas 2011), and expert knowledge on the compatibility of the presence of particular plant species within plant communities mapped all throughout the study area by FMS. Only plant resources were considered, due to the lack of information for other foraging resources (e.g. wild ungulates, insects). In any case, we believe this variable is a good estimator of foraging resources given that plant matter represents the most important food for brown bears (Clevenger et al. 1992; Naves et al. 2006; Ciucci et al. 2014). Year-round map of foraging resources was estimated as the sum of the seasonal foraging resources. We calculated the focal mean (i.e. mean value for each cell location within a specific neighborhood depending on the extent of measurement) of seasonal and total year-round foraging resources at the nine scales mentioned above.

#### Shelter

Brown bears have high dependence on forest cover (Clevenger et al. 1992). Beyond food availability, previous studies have highlighted the importance of forest and shrublands in term of shelters and habitat continuity (Gómez-Manzanedo et al. 2012; Mateo-

**Table 1** Environmental variables used for analyzing brown bear habitat suitability

Metric	Description	Data source	Unit
Foraging resources			
SpFR	Focal mean of spring foraging resources	LiDAR + FMS + specific models	%
SuFR	Focal mean of summer foraging resources	LiDAR + FMS + specific models	%
AFR	Focal mean of autumn foraging resources	LiDAR + FMS + specific models	%
WFR	Focal mean of winter foraging resources	LiDAR + FMS + specific models	%
TotFR	Focal mean of total (year-round) foraging resources (sum of foraging resources in each season)	LiDAR + FMS + specific models	%
Shelter			
FCC	Focal mean of forest canopy cover	LiDAR	%
FHei	Focal mean of forest height	LiDAR	m
ForCI	Cohesion index of forests	LiDAR	Dimensionless
ShrubCI	Cohesion index of shrubland	FMS	Dimensionless
Human pressure			
BuildDens	Building density	CNIG	Buildings/km <sup>2</sup>
HwDens	Highways density	OSM	km/km <sup>2</sup>
RoadDens	Conventional roads density	OSM	km/km <sup>2</sup>

Focal mean is the mean value of each variable within a specific neighborhood (depending on the scale of measurement) around each location. Foraging resources were expressed as percentage of the maximum possible resources in a location

FMS forest map of Spain, CNIG Spanish Geographic National Institute, OSM open street map

Sánchez et al. 2014) as they provide cover for roosting, escaping dangers, rearing young, and loafing. In addition, in these forest areas human pressures are fewer Palomero et al. 2011). Therefore, we used variables of forest and shrubland structure as potential surrogates for brown bears shelter (Table 1). LiDAR data provided estimates of forest canopy cover and forest height. We calculated the focal mean of the previous variables across the nine assessed scales. In order to evaluate the effect of connectedness of forest and shrubland cover, we also calculated the cohesion index for these two cover types in FRAGSTATS 4.2 (McGarigal et al. 2012). Forest area was obtained from LiDAR data (forest canopy cover  $\geq 30\%$ ). Cohesion of forest and cohesion of shrubland were evaluated only for seven extents (excluding 32 and 64 km) to reduce “boundary effects”; the cohesion index cannot be calculated for cells located at a distance from the edge of the study area smaller than the considered extent, which would have excluded a large proportion of the study area (including locations with significant densities of brown bear presence records) for these large extents of 32 and 64 km; see McGarigal et al. (2012).

### Human pressure

We included density of buildings and transport infrastructures as predictors of human pressure (Table 1). Buildings were extracted from a topographic map developed by Spanish Geographic National Institute (CNIG) and transport infrastructures from open street map (OSM, [www.openstreetmap.org](http://www.openstreetmap.org)). We divided transport infrastructures in highways and conventional roads to try to assess potential different effects depending on traffic volume and physical restrictions on bear distribution. The density of these elements was evaluated at the proposed nine scales.

### Modelling seasonal changes in habitat use

First, univariate models were performed to identify in every season (astronomical seasons were used) the operational scale, i.e. the spatial extent at which each environmental variable was most strongly related to brown bear occurrence (e.g., Grand et al. 2004; Mateo-Sánchez et al. 2014). We used *lrm* and *penrtrace* functions from the *rms* package (Harrell 2014) in the R

environment for statistical computing (R Core Team 2014) to fit penalized logistic regression models (Harrell 2001) with each predictor as a single linear term. For every season we chose the operational scale (i.e., scale with best performance) of each predictor using Akaike's Information Criterion (AIC; Johnson and Omland 2004). Twenty thousand random pseudo-absence points were drawn inside limits of the study area (cell size = 1 ha). The pseudo-absences were the same for every single model.

Secondly, multi-scale models (e.g. Grand et al. 2004; Shirk et al. 2012; Wasserman et al. 2012) were developed to assess the effect of each predictor in brown bear distribution. According to the results of the univariate models, we developed for each season a model combining environmental variables at their specific operational scales. For a meaningful comparison and understanding of changes in habitat use between seasons, we used in all the cases the full set of explanatory variables. Except for seasonal changes in foraging resources, explanatory variables were treated as static across seasons. We developed penalized logistic regression models with linear terms only and without interactions among predictors. We used *lrm* and *penrtrace* functions to fit the logistic regressions models. We assessed the predictive performance of multi-scale models using the area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997) estimated with ten-fold cross-validation. As the main objective of these models is to rank sites according to the suitability for the species, AUC is a good option because it measures discrimination, i.e., the probability that the predicted value is higher in a presence point than in a pseudo-absence point, both picked at random.

#### Modelling temporal changes in habitat use

Data analysis followed the same procedures and set of explanatory variables as for seasonal models (i.e., univariate models to select the operational scale of each predictor and multi-scale models to assess predictor influence). We separately used locations of the two periods 2000–2004 and 2005–2010 (instead of seasonal locations), as well as locations for the entire period 2000–2010, and used in all cases the same set of explanatory variables. We used year-round foraging resources (foraging resources were not considered separately for each season in this multi-annual

analysis). Similarly, we considered that variables did not change over the studied period, since important land-use changes have not happened in the study area in the assessed ten-year period, particularly in comparison with the sharp increase experienced by the bear population, which is mainly the result of its protection status for the last three decades and related changes in human attitudes towards bears.

## Results

### Seasonal changes in habitat use

The results of the univariate models showed a similar pattern of operational scales across seasons (Table 2). Environmental variables related to foraging resources affected bear habitat suitability at broad scales (16 km in most cases), especially during fall. Variables related to human pressure also affected habitat suitability at broad scales. However, potential predictors of bear shelter showed more discrepancy: shrubland cohesion (ShrubCI) presented the highest AIC values at a large extent (16 km), while the highest AIC for forest predictors was mainly found at a fine or medium scale (1 km in most cases). All the set of evaluated multivariate models showed good performance, with AUC ranging from 0.897 to 0.938. The AUC values were higher ( $p < 0.001$ ) in fall and winter than in spring and summer (Table 3). As we expected, independent variables related to human pressure had a negative effect on bear habitat suitability (Table 3). Building density had an important negative effect in all seasons, especially in spring. Road density did not have a significant effect in spring and fall, but it affected negatively in summer and winter. Highway density had a more negative effect on habitat use than road density (higher coefficients in absolute value), but it did not influence habitat suitability in winter. Habitat suitability was significantly related to foraging resources in all seasons (Table 3). Variables related to bear shelter had a general positive effect on bear habitat suitability, particularly shrubland cohesion (high positive coefficients), but forest height did not influence significantly habitat use in summer and winter. In like manner, seasonal changes were also noticeable in the spatial pattern of habitat suitability (Fig. 2). Habitat suitability showed the most extensive

**Table 2** Operational scale (km) for each environmental variable and season/period used for analyzing brown bear habitat suitability

Predictor	Spring	Summer	Fall	Winter	Year-round (2000–2010)	2000–2004	2005–2010
SpFR	16						
SuFR		16					
AFR			32				
WFR				16			
TotFR					16	16	16
FCC	1	0.5	1	1	1	1	1
FHei	0.5	0.5	0.5	0.5	0.5	0.5	0.5
ForCI	16	16	4	1	16	16	16
ShrubCI	16	16	16	16	16	16	16
BuildDens	16	16	16	16	16	16	16
HwDens	16	16	16	16	16	16	16
RoadDens	16	16	16	16	16	16	16

Seasonal results correspond to the entire period 2000–2010. See Table 1 for variable description

pattern in spring and summer, and the most local pattern in winter.

Temporal changes in habitat use

Selected operational scales followed the same trend for both partial periods (2000–2004 and 2005–2010) and for the entire 2000–2010 period and broadly coincided with seasonal patterns (Table 2). Foraging resources affected bear habitat suitability at broad scales (16 km). Human pressure variables also

affected habitat suitability at large extents (16 km). Shelter variables influenced at broad scales in some cases (ShrubCI, ForCI) and at fine scales (0.5–1 km) in others (FCC, FHei).

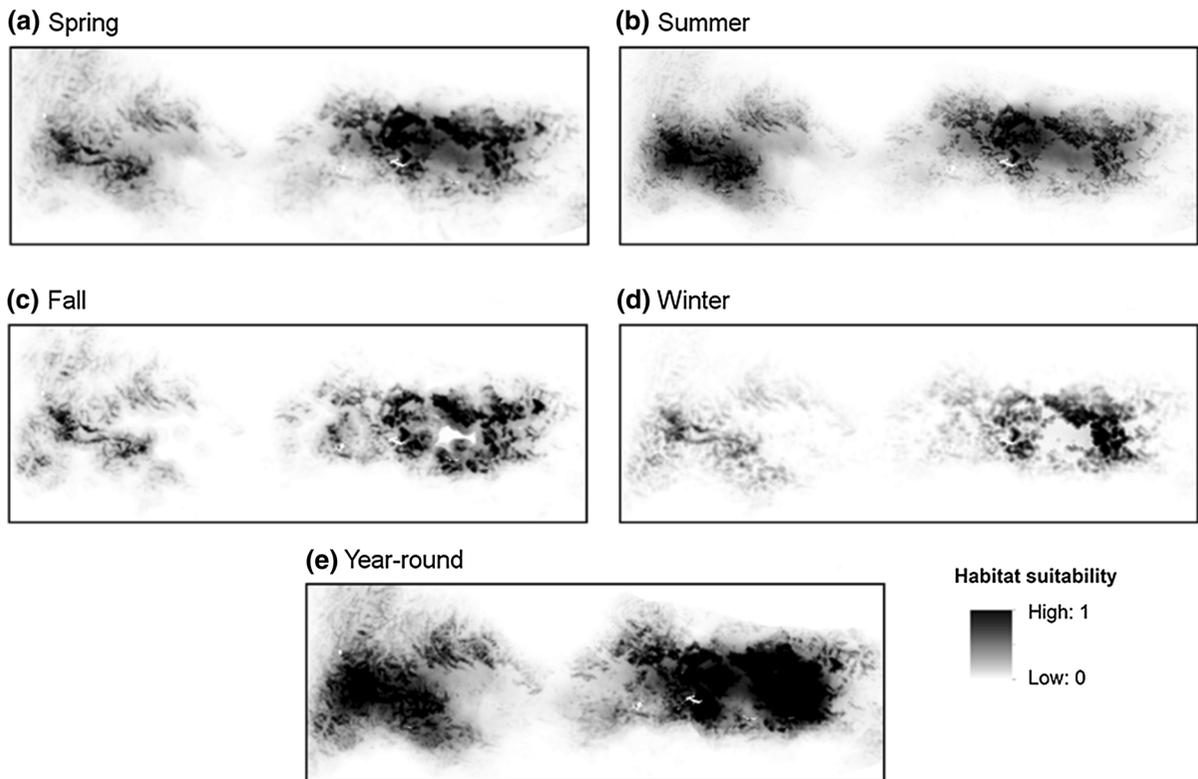
All the evaluated multivariate models showed good model performance (AUC ranging from 0.900 to 0.947) (Table 4). AUC values were remarkably higher ( $p < 0.001$ ) in the “constrained” period (2000–2004) than in the “growth” (population expansion) period (2005–2010). The synoptic pattern of habitat suitability was also wider in the second period of population

**Table 3** Seasonal changes in habitat use as inferred from seasonal presence records for the entire period 2000–2010

Predictor	Spring		Summer		Fall		Winter		Total (year round)	
	Scale	Coef	Scale	Coef	Scale	Coef	Scale	Coef	Scale	Coef
SFR	16	0.337***	16	0.744***	32	0.697***	16	1.108***	16	1.165***
FCC	1	0.305***	0.5	0.332***	1	0.312***	1	0.357***	1	0.163***
FHei	0.5	0.129*	0.5	-0.017	0.5	0.286***	0.5	0.107	0.5	0.291***
ForCI	16	0.768***	16	0.494***	4	0.829***	1	0.559***	16	0.179***
ShrubCI	16	1.341***	16	1.759***	16	2.729***	16	2.833***	16	2.156***
BuildDens	16	-2.269***	16	-1.717***	16	-1.694***	16	-1.48***	16	-1.171***
HwDens	16	-0.616***	16	-0.51***	16	-1.429***	16	0.079	16	-0.616***
RoadDens	16	-0.045	16	-0.196*	16	-0.205	16	-0.883***	16	0.051
AUC	0.897		0.901		0.928		0.938		0.910	

See Table 1 for variable description. SFR corresponds to seasonal foraging resource and varies depending of the season/period analyzed

Significance levels: \*\*\* <0.001, \*\* <0.01, \* <0.05



**Fig. 2** Habitat suitability maps provided by the optimized multi-scale model for every season: **a** spring, **b** summer, **c** fall, **d** winter and **e** year-round. Seasonal and year-round results correspond to the entire period 2000–2010. See Fig. 1 for the location of the area here shown

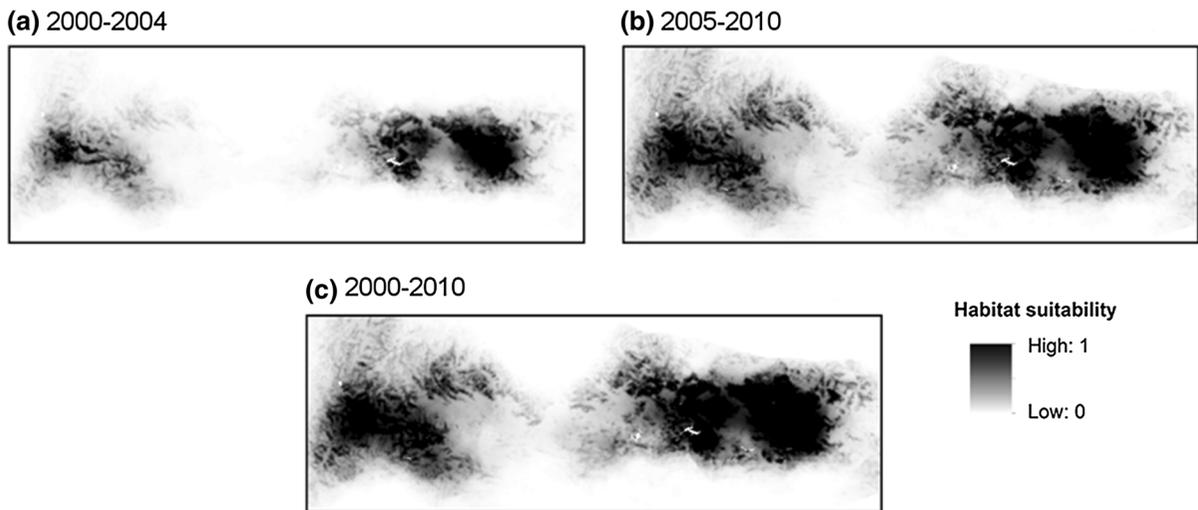
expansion and more concentrated in core areas during the first period with smaller population size (Fig. 3). Building density had an important negative effect during all seasons, especially in the “constrained” period (Table 4). Highway density had a significant negative effect only in the “growth” period. Habitat suitability was significantly related to foraging resources during all the studied periods (Table 4). Potential predictors of bear shelter also had a positive effect on habitat use, especially shrubland cohesion.

## Discussion

Robustness in operational scales across seasons and time periods

Distribution of species is driven by processes linked to several levels of ecological complexity, and therefore expressed at different scales (Vicente et al. 2011).

Previous research (Mateo-Sánchez et al. 2014) showed that explicitly optimizing the scale of habitat suitability models considerably improved single-scale modeling for brown bears in terms of (i) model performance and spatial prediction and (ii) avoiding an oversimplification and lack of appreciation of details that were blurred or missed in habitat models conducted at a single scale. Our results support the conclusion by Mateo-Sánchez et al. (2014) that brown bears respond to environmental factors at different scales, but provide further new insights into the influence of processes underlying temporal and spatial variations in habitat use. We found that operational scales were scarcely affected by the different ways in which bears use habitat due to seasonal changes or population status. This suggests that bears may have a scale of perception of the environment not mediated by changes in species distribution or trends, despite the fact that several authors have related operative scales to movement ranges of the organism (Wiens 1989;



**Fig. 3** Habitat suitability maps provided by the optimized multi-scale model for every period: **a** 2000–2004, **b** 2005–2010 and **c** 2000–2010. Map (c) in this figure is the same as map (e) in Fig. 2. See Fig. 1 for the location of the area here shown

**Table 4** Temporal changes in habitat use

Predictor	2000–2004		2005–2010		Total (2000–2010)	
	Scale	Coef	Scale	Coef	Scale	Coef
TotFR	16	1.607***	16	0.978***	16	1.165***
FCC	1	0.177*	1	0.139**	1	0.163***
FHei	0.5	0.243***	0.5	0.314***	0.5	0.291***
ForCI	16	0.208*	16	0.182***	16	0.179***
ShrubCI	16	3.457***	16	2.003***	16	2.156***
BuildDens	16	−2.996***	16	−1.083***	16	−1.171***
HwDens	16	0.200	16	−0.704***	16	−0.616***
RoadDens	16	0.489***	16	0.749	16	0.051
AUC	0.947		0.900		0.910	

See Table 1 for variable description

Significance levels:  
 \*\*\* <0.001, \*\* <0.01,  
 \* <0.05

Vos et al. 2001; Dungan et al. 2002). We did not find evidence that different activity patterns potentially due to environmental conditions, population trends, nutritional or reproductive status impacted on operative scales that rule habitat relationships. A plausible explanation might be that in brown bears the extensive seasonal movements (such as mating or dispersal movements beyond currently occupied areas) are mostly undertaken by males while females are typically philopatric (Swenson et al. 1998), while in our study the available presence records did not allow for a differentiation of the genders. More detailed information (e.g., age and gender of the individuals in the species occurrence records, tracking telemetry) and additional research may be necessary to shed further

light on the influence of the habitat use during these movements on operational scales. It has to be noted, however, that so far there has been very little empirical evidence of the effects of home range size or dispersal distance on the operational scales (Desrochers et al. 2010; Fisher et al. 2011). In any case we recognize that these aspects might be crucial when selecting the range of scales at which landscape variables should be measured to identify accurate and biologically-justified operational scales.

Additionally, for periods when habitat use is more limited (i.e., winter or period with smaller population size) and thus local selection could be expected to be stronger (more restrictive), our results showed that brown bears also have a large-scale perception of

factors related to habitat configuration, food resource and human disturbance, similar to other periods when habitat use is more extensive. Whereas other factors related to forest characteristics (such as forest cover and height) were always supported at the finest scales regardless the season or population status. This result suggests that both large-scale and fine-scale factors contribute to determine, although to different degrees, brown bear perception and use of habitat.

Some similar dominant drivers of brown bear habitat suitability across seasons and time periods

Landscape configuration together with human pressure and food availability appeared to be dominant drivers for brown bear habitat selection whatever the period of the year and the status/size of the population, suggesting the importance of large extents of forest cover with low human footprint. Particularly, our results highlighted the importance of landscape with extent of connected shrubland at broad scales without seasonal or temporal differences, even showing a stronger relationship with bear occurrence than foraging resources and cohesion of forest areas. This may suggest the importance of shrubland as linkage areas through which bears can move between other habitat patches and their potential contribution to habitat suitability in terms of shelter, matrix permeability and habitat continuity.

Human pressure: building density more influential than roads

Medium and large mammals generally suffer strong human pressures (Cardillo et al. 2005) and therefore they are more abundant in areas with low human footprint (Woodroffe 2000). In our case study, brown bears showed a marked avoidance of predictors of human pressure at broad scales. Interestingly, these predictors did not contribute to the multi-scale models prediction in the same way. The density of buildings was the most influential variable in the group and showed a strong negative relationship with bear habitat. This was also consistent with previous habitat studies (Naves et al. 2003; Apps et al. 2004; Mateo-Sánchez et al. 2014), but our results furtherly showed that the avoidance is similar for all the seasons and periods with different population size. This suggests that brown bear strongly avoids areas in the landscape

to a considerable distance (16 km) away from dense human settlements.

However, linear infrastructures provided less predictive ability and different contribution according to the season and size of the population. Highways showed much higher effect than roads; the latter one only had significant effect in summer and winter. This fact may be related to the species space requirements. Summer and winter are two seasons with a lower activity and smaller home ranges (Huber and Roth 1993), thus individuals may select more localized areas. This aspect is also illustrated by the spatial pattern of habitat suitability, with optimal areas constrained to a comparatively lower number of high quality patches in the core areas in winter in comparison to a wider range of suitable areas in seasons with a broader habitat use (i.e., spring) and to the year-round habitat use (Fig. 2). Interestingly, highways did not influence multi-scale model prediction in winter whereas conventional roads did. This result may be due to the fact that the more extensive network of conventional roads may affect bear habitat requirements, whereas highways are scarcer and their spatial distribution in the landscape may not influence the more remote and localized used by bears in that season. The same trend was observed in the first analyzed period with smaller population size in which individuals were constrained to the areas with best habitat quality and low human influence, as is also reflected in the habitat suitability spatial pattern (Fig. 3a).

Food resource as a key factor in habitat use

Landscape composition was mostly introduced in the models in terms of food availability since it has been advocated as pervasive predictors of animal movement, space use and habitat selection (Fretwell and Lucas 1970; Fryxell et al. 2004; Ciudad et al. 2009; Van Beest et al. 2011). Food resource added predictive power to all the multi-scale models and showed a higher contribution in year-round models, no matter the status and distribution of the population, suggesting that food resources are critical regulating factors affecting individual growth and population density (Mattson et al. 2004). This finding shows that bears are well suited to forage-based definitions of habitat quality (Nielsen et al. 2010). Seasonal food availability is particularly important for bears due to high nutritional demands in periods such as hyperphagia (i.e.,

last part of summer and fall when individuals accumulate fat to survive winter; Berland et al. 2008) and during spring, particularly for females with cubs (Rode and Robbins 2000). However, the contribution of food resource to seasonal multi-scale models was variable along the seasons and did not show this pattern. Food resources had also a stronger contribution to the multi-scale seasonal models in summer and winter (see Table 3). This furtherly supports our conclusion that due to the more reduced (localized) use of landscape in these seasons, brown bear occurrence would be associated with more specialized habitat requirements and therefore distributed into more localized highest quality spots (Fig. 2d). Suitable habitat is restricted to places with forage supplies and shelter, more scarce in winter (Fig. 2d) and more spread in summer (Fig. 2b). However, the extent of suitable habitat increased in the other seasons (e.g. spring) in which individuals required to use a wider variety of habitat resources as shown in Fig. 2a. In other words, the species may exhibit more generalist traits, as shown for other species, under environmental or density changes (Colles et al. 2009; Barnagaud et al. 2011) and seasonal food availability might lose predictive ability. Even in periods in which foraging is crucial, such as hyperphagia, and in spring, the broader use of resources might reduce the inferred strength of the foraging resource variable in the habitat models.

Shelter and forest structure are important at fine spatial scales

Habitat quality attributes related to forest structure were significant at fine scales in most of the multi-scale models. Mature stands may be important not only for their higher productivity of food resources (Apps et al. 2004), but also for their suitability to be used as shelter areas (Clevenger et al. 1997). Forest height was significant for seasonal habitat use in fall and summer. During fall the effect may be correlated to foraging use of these habitats due to their potential higher fruit production and during summer to refuge and thermal regulation (Apps et al. 2004). Forest canopy cover was consistently a good predictor of bear occurrence along the seasons and periods, suggesting that forests with higher canopy cover provide more protection to bears. These findings are consistent with previous ecological knowledge on habitat selection of this species in the study area. For example, Clevenger

(1991) found that brown bear in the Cantabrian Range was largely dependent on forest cover. Naves et al. (2003) and Mateo-Sánchez et al. (2014) also found that forest cover was positively related to habitat use. However, this conclusion differs from other studies for brown bear in other study areas (e.g. Canada), where canopy cover seemed to be inversely related to use, likely favoring other food resources in more open areas. A plausible explanation for this difference is the nature and size of the study area. The Cantabrian Range has, as most of the Iberian Peninsula, an old history of human uses and bear persecution. In addition, in this area humans and bears cohabit in a relatively small extent where closed forest cover may provide crucial protection from humans. On the contrary, other landscapes in North America or North Scandinavia with very low human pressure over large areas might offer remote and inaccessible lands regardless of canopy closure.

Influence of population size and seasonal resources for multi-scale models predictive ability: the more spread the population is, the more difficult prediction becomes

We found that multi-scale models' ability to predict brown bear occupancy was influenced by the status and size of this population as well as by seasonal changes. In the early years with small population size, presumably quite below the carrying capacity of the available habitat in the core population nuclei, bear occurrence was associated with a narrow range of habitat characteristics (hence more predictable) as apparent from the spatial distribution of bear habitat (Fig. 3a). However, the population increase and potential saturation in parts of the core nuclei might have resulted in the newly expanding populations using an increased variety of land covers and other environmental characteristics in the landscape. This broader range and diversity of environmental characteristics may force individuals to be more plastic (more generalist in their habitat preferences) when selecting new territories outside the original (and saturated) core populations, including settlement into more heterogeneous and lower-quality areas (Fig. 3b), agreeing with recent results for other mammal species in Spain such as the Iberian lynx (Gastón et al. 2015). Such trend would translate into reduced model prediction ability for the period 2005-2010 (that with an expanding species range).

This finding is congruent with McFarland et al. (2014), who found that multi-scale species distribution models produced poor estimations for a bird species with a growing population.

Similar considerations apply to seasonal models, which showed higher predictive ability in winter, when the home ranges are smaller and use of resources is confined to more localized areas. In contrast, predictions were weaker in spring, when longer distance dispersal and mating trigger the use of suboptimal habitat. Good predictions for fall might be given by a broader use of resources than in winter but narrower than in spring, considering that in fall availability and reachability of high quality habitat is needed due to nutritional requirements (i.e., hyperphagia).

In any case, all the multi-scale models in this study outperformed previous multi-scale models for the species in the study area (Mateo-Sánchez et al. 2014). Optimal multi-scale models in the previous study by Mateo-Sánchez et al. (2014) included variables related to landscape composition (percentage of the landscape occupied by forest), human disturbance and canopy cover with AUC = 0.862, compared to 0.910 of the year-round model in this study. This remarkable increase ( $p < 0.001$ ) in model performance may be due to (i) the direct quantification of foraging resources as a predictive variable (including seasonal and year-round estimates) and (ii) the use of a finer spatial resolution of the environmental data, particularly LiDAR data on vegetation structure, concurring with the results from previous single-scale habitat studies (Tattoni et al. 2012; Zellweger et al. 2014). Additional comparative research should however be tackled to specifically clarify how different data on forest cover may influence inferences and predictive power of multi-scale habitat suitability models.

## Conclusions

Multi-scale habitat models have shown to accurately predict areas where species can meet their ecological requirements, and enable researchers to reliably understand the species-habitat relationships. However, very little was known about how the spatiotemporal changes in species distributions may affect the operational scales and the inferred habitat relationships. As shown in this study, operative scales appeared to be robust across variations in bear habitat use and distribution due to

seasonal changes and population increase, showing a likely stable perception of environment. However, the hierarchy and strength of factors influencing habitat relationships is different depending on the distinctive use of seasonal and temporal resources. Similarly, key differential factors among seasons, such as seasonal food resource, are crucial to provide more accurate and informative habitat suitability models. Here we intended to highlight that the understanding of multi-scale behavioral responses by species to spatial patterns that continually shift over time may be essential to produce reliable species distribution modelling that feed conservation measures. We admit that our habitat models could be further strengthened in two directions. First, by explicitly accounting for temporal changes in landscape structure (e.g. changes in forest cover or structure through time), besides the considered changes in population status. Second, through more detailed information about brown bear use of the landscape, particularly through movement data gathered through a sufficiently large set of GPS collars for individuals of different age, gender and condition. Regardless these potential directions for future improvements, we hope that our study has contributed to the understanding of multi-scale species-habitat relationships in dynamic landscapes and populations, and hope to motivate further research on this topic with important implications in landscape ecology. Finally, our study provides the most detailed (spatially and temporally) habitat models available so far for the endangered brown bear populations in the Cantabrian Range, therefore being of considerable value to support conservation strategies aiming to ensure the persistence of this emblematic species in the Iberian Peninsula.

**Acknowledgments** Funding was provided by the Spanish Ministry of Science and Innovation research grant GEFOUR (AGL2012-31099) and Technical University of Madrid. We are also grateful to the Regional Administration involved in the brown bear management: Junta de Castilla y León, Gobierno de Cantabria, Principado de Asturias and Xunta de Galicia for providing data. Thanks also to the valuable support provided by Fundación Oso Pardo.

## References

- Anderson DP, Forester JD, Turner MG, Frair JL, Merrill EH, Fortin D, Mao JS, Boyce MS (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecol* 20(3):257–271

- Apps CD, McLellan BN, Woods JG, Proctor MF (2004) Estimating grizzly bear distribution and abundance relative to habitat and human influence. *J Wildl Manag* 68(1): 138–152
- Ballesteros F, Palomero G (2012) Conectividad, demografía y conservación del oso pardo Cantábrico. In: San Miguel A, Ballesteros F, Blanco JC, Palomero G (eds) *Manual de buenas prácticas para la gestión de corredores oseros en la Cordillera Cantábrica*. Fundación Oso Pardo. Ministerio de Agricultura, Alimentación y Medio Ambiente. Serie Especies Amenazadas, Madrid, pp 21–33
- Ballesteros F, Martín B, Blanco JC (2012) Calidad de hábitat y presencia de osos en el corredor interpoblacional. In: San Miguel A, Ballesteros F, Blanco JC, Palomero G (eds) *Manual de buenas prácticas para la gestión de corredores oseros en la Cordillera Cantábrica*. Fundación Oso Pardo. Ministerio de Agricultura, Alimentación y Medio Ambiente. Serie Especies Amenazadas, Madrid, pp 33–56
- Barnagaud JY, Devictor V, Jiguet F, Archaux F (2011) When species become generalists: on-going large-scale changes in bird habitat specialization. *Global Ecol Biogeogr* 20(4):630–640
- Berland A, Nelson T, Stenhouse G, Graham K, Cranston J (2008) The impact of landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta, Canada. *For Ecol Manag* 256(11):1875–1883
- Börger L, Franconi N, Ferretti F, Meschi F, De Michele G, Gantz A, Coulson T (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am Nat* 168(4):471–485
- Bradley BA, Wilcove DS, Oppenheimer M (2010) Climate change increases risk of plant invasion in the Eastern United States. *Biol Invasions* 12(6):1855–1872
- Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309(5738):1239–1241
- Ciucci P, Tosoni E, Di Domenico G, Quattrociocchi F, Boitani L (2014) Seasonal and annual variation in the food habits of Apennine brown bears, central Italy. *J Mammal* 95(3):572–586
- Ciudad C, Robles H, Matthysen E (2009) Postfledging habitat selection of juvenile middle spotted woodpeckers: a multiscale approach. *Ecography* 32:676–682
- Clevenger AP (1991) Selección de hábitat. In: Clevenger AP, Purroy FJ (eds) *Ecología del oso pardo en España*. Madrid. Museo Nacional de Ciencias Naturales, CSIC (Monografías 4), pp 73–84
- Clevenger A, Purroy F, Pelton M (1992) Brown bear (*Ursus arctos* L.) habitat use in the Cantabrian Mountains, Spain. *Mammalia* 56(2):203–214
- Clevenger AP, Purroy FJ, Campos MA (1997) Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. *Biol Conserv* 80(1):17–22
- Colles A, Liow LH, Prinzing A (2009) Are specialists at risk under environmental change? Neocological, paleoecological and phylogenetic approaches. *Ecol Lett* 12(8): 849–863
- Delibes M (1999) Osos y madroños. *Biología* 39:62–63
- Desrochers A, Renaud C, Hochachka WM, Cadman M (2010) Area-sensitivity by forest songbirds: theoretical and practical implications of scale-dependency. *Ecography* 33:921–931
- Dungan JL, Perry JN, Dale MRT, Legendre P, Citron-Pousty Fortin M-J, Jakomulska A, Miriti M, Rosenberg MS (2002) A balanced view of scale in spatial statistical analysis. *Ecography* 25(5):626–640
- Fernandez-Calvo I, Naves J, Fernandez-Gil A, Iglesias JM (2001). Variación interanual en la dieta del oso pardo cantábrico (*Ursus arctos*) y su relación con la disponibilidad. In: V National Meeting of the Spanish Society for study and conservation of mammals. SECEM, Vitoria, Spain, pp 64–65
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24(01):38–49
- Fisher JT, Anholt B, Volpe JP (2011) Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecol Evol* 1:517–528
- Fortin M-J, James PMA, MacKenzie A, Melles SJ, Rayfield B (2012) Spatial statistics, spatial regression, and graph theory in ecology. *Spat Stat* 1:100–109
- Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor* 19(1):16–36
- Fryxell JM, Wilmshurst JF, Sinclair AR (2004) Predictive models of movement by Serengeti grazers. *Ecology* 85(9):2429–2435
- García P, Lastra J, Marquín J, Nore C (2007) Detailed model of shelter areas for the Cantabrian brown bear. *Ecol Inform* 2(4):297–307
- Gastón A, García-Viñas JA (2011) Modelling species distributions with penalised logistic regressions: a comparison with maximum entropy models. *Ecol Model* 222(13): 2037–2041
- Gastón A, Blázquez-Cabrera S, Garrote G, Mateo-Sánchez MC, Beier P, Simón MA, Saura S (2015). Contrasting responses to different agricultural covers and dispersal plasticity of woodland species: the case of the endangered Iberian lynx
- Gómez-Manzanedo M, Urchaga A, Roig S, San Miguel A (2012) Gestión de la vegetación arbustiva y herbácea. In: San Miguel A, Ballesteros F, Blanco JC, Palomero G (eds) *Manual de buenas prácticas para la gestión de corredores oseros en la Cordillera Cantábrica*. Fundación Oso Pardo. Ministerio de Agricultura, Alimentación y Medio Ambiente. Serie Especies Amenazadas, Madrid, pp 101–140
- Grand J, Buonaccorsi J, Cushman SA, Griffin CR, Neel MC (2004) A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. *Conserv Biol* 18(4):1063–1077
- Harrell FE (2001) *Regression modeling strategies: with applications to linear models, logistic regression and survival analysis*. Springer, New York
- Harrell FE (2014) rms: regression modeling strategies. R package version 4.2-1. <http://cran.r-project.org/packages=rms>
- Holland J, Fahrig L (2000) Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. *Agric Ecosyst Environ* 78(2):115–122
- Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. *Bioscience* 54(3):227–233

- Huber D, Roth HU (1993) Movements of European brown bears in Croatia. *Acta Theriol* 38:151–159
- Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? *Landscape Ecol* 27(7):929–941
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61(1):65–71
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Kie JG, Bowyer RT, Nicholson MC, Boroski BB, Loft ER (2002) Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83(2):530–544
- Koreň M, Find'ó S, Skuban M, Kajba M (2011) Habitat suitability modelling from non-point data: the case study of brown bear habitat in Slovakia. *Ecol Inform* 6(5):296–302
- Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59(2):253–260
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73(6):1943–1967
- Marquín J (2002) Delimitación de áreas críticas para el oso pardo y cartografía de calidad de hábitat. Instituto de Recursos Naturales y Ordenación del Territorio, Universidad de Oviedo. Consejería de Medio Ambiente. Gobierno del Principado de Asturias
- Mateo-Sánchez MC, Cushman SA, Saura S (2014) Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). *Int J Geogr Inf Sci* 28(8):1531–1546
- Mattson DJ, Barber K, Maw R, Renkin R (2004) Coefficients of productivity for Yellowstone's grizzly bear habitat. US Department of the Interior, US Geological Survey
- McFarland TM, Grzybowski JA, Mathewson HA, Morrison ML (2014) Presence-only species distribution models to predict suitability over a long-term study for a species with a growing population. *Wildl Soc Bull* 39:218–224
- McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McGaughey RJ, Carson WW (2003) Fusing LIDAR data, photographs, and other data using 2D and 3D visualization techniques. In: Proceedings of terrain data: applications and visualization—making the connection, October 28–30, pp 16–24
- Ministerio de Fomento (2015) Plan Nacional de Ortofotografía Aérea. Instituto Geográfico Nacional. [www.pnoa.ign.es](http://www.pnoa.ign.es)
- Naves J, Palomero G (1993) El oso pardo en España (*Ursus arctos*). ICONA, Madrid
- Naves J, Wiegand T, Fernández AF, Stephan T (1999) Riesgo de extinción del oso pardo cantábrico. La población occidental. Fundación Oso de Asturias, Oviedo
- Naves J, Fernández-Gil A, Delibes M (2001) Effects of recreation activities on a brown bear family group in Spain. *Ursus* 12:135–140
- Naves J, Wiegand T, Revilla E, Delibes M (2003) Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conserv Biol* 17(5):1276–1289
- Naves J, Fernández-Gil A, Rodríguez C, Delibes M (2006) Brown bear food habits at the border of its range: a long-term study. *J Mammal* 87(5):899–908
- Nielsen SE, McDermid G, Stenhouse GB, Boyce MS (2010) Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biol Conserv* 143(7):1623–1634
- Palomero G (1995) Winter activity of the brown bear in the Cantabrian Mountains (Spain). In: Abstracts of the 10th tenth international conference on bear research and management, Mora, Sweden, 11–14th September
- Palomero G, Ballesteros F, Blanco JC, García-Serrano A, Herrero J, Nores C (2011) Osas, el comportamiento de las osas y sus crías en la Cordillera Cantábrica, 2nd edn. Fundación Oso Pardo, Fundación biodiversidad, Madrid
- Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27(3):285–298
- Pope SE, Fahrig L, Merriam HG (2000) Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81(9):2498–2508
- Posillico M, Meriggi A, Pagnin E, Lovari S, Russo L (2004) A habitat model for brown bear conservation and land use planning in the central Apennines. *Biol Conserv* 118(2):141–150
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>. Version 3.1.2
- Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23(4):466–478
- Rode K, Robbins C (2000) Why bears consume mixed diets during fruit abundance. *Can J Zool* 78(9):1640–1645
- Savignac C, Desrochers A, Huot J (2000) Habitat use by pileated woodpeckers at two spatial scales in eastern Canada. *Can J Zool* 78(2):219–225
- Schaefer JA, Messier F (1995) Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18(4):333–344
- Shirk AJ, Wasserman TN, Cushman SA, Raphael MG (2012) Scale dependency of American marten (*Martes americana*) habitat relations. In: Aubry KB, Zielinski WJ, Raphael MG, Proulx G, Buskirk W (eds) Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, Ithaca, pp 269–283
- Swenson JE, Sandegren F, So-Derberg A (1998) Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *J Anim Ecol* 67(5):819–826
- Tattoni C, Rizzolli F, Pedrini P (2012) Can LiDAR data improve bird habitat suitability models? *Ecol Model* 245:103–110
- Triantis KA, Mylonas M, Lika K, Vardinoyannis K (2003) A model for the species–area–habitat relationship. *J Biogeogr* 30(1):19–27
- Urban DL (1987) Landscape ecology. *Bioscience* 37:119–127
- Van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A (2011) What determines variation in home range size

- across spatiotemporal scales in a large browsing herbivore? *J Anim Ecol* 80(4):771–785
- Vicente J, Randin CF, Gonçalves J, Metzger MJ, Lomba A, Honrado J, Guisan A (2011) Where will conflicts between alien and rare species occur after climate and land-use change? A test with a novel combined modelling approach. *Biol Invasions* 13(5):1209–1227
- Vicente JR, Gonçalves J, Honrado JP, Randin CF, Pottier J, Broennimann O, Lomba A, Guisan A (2014) A framework for assessing the scale of influence of environmental factor on ecological patterns. *Ecol Complex* 20:151–156
- Vos CC, Verboom J, Opdam PF, Ter Braak CJ (2001) Toward ecologically scaled landscape indices. *Am Nat* 157(1): 24–41
- Wasserman TN, Cushman SA, Wallin DO, Hayden J (2012) Multi scale habitat. Relationships of *Martes americana* in northern Idaho, USA. USDA forest service RMRS research paper RMRS-RP-94
- Weaver JE, Conway TM, Fortin M-J (2012) An invasive species' relationship with environmental variables changes across multiple spatial scales. *Landscape Ecol* 27: 1351–1362
- Wiegand T, Naves J, Stephan T, Fernández A (1998) Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecol Monogr* 68(4): 539–570
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. *Anim Conserv* 3(2):165–173
- Zellweger F, Morsdorf F, Purves RS, Braunisch V, Bollmann K (2014) Improved methods for measuring forest landscape structure: LiDAR complements field-based habitat assessment. *Biodivers Conserv* 23(2):289–307
- Zollner PA (2000) Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecol* 15(6):523–533