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RESEARCH ARTICLE

Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and *Martes foina*) in the northern Iberian Peninsula

Maria Vergara · Samuel A. Cushman ·
Fermín Urra · Aritz Ruiz-González

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Abstract

Context Multispecies and multiscale habitat suitability models (HSM) are important to identify the environmental variables and scales influencing habitat selection and facilitate the comparison of closely related species with different ecological requirements.
Objectives This study explores the multiscale relationships of habitat suitability for the pine (*Martes martes*) and stone marten (*M. foina*) in northern Spain to evaluate differences in habitat selection and scaling, and to determine if there is habitat niche displacement when both species coexist.
Methods We combined bivariate scaling and maximum entropy modeling to compare the multiscale habitat selection of the two martens. To optimize the HSM, the performance of three sampling bias correction methods at four spatial scales was explored. HSMs were compared to explore niche differentiation between species through a niche identity test.
Results The comparison among HSMs resulted in the detection of a significant niche divergence between species. The pine marten was positively associated with cooler mountainous areas, low levels of human disturbance, high proportion of natural forests and well-connected forestry plantations, and medium-extent agroforestry mosaics. The stone marten was positively related to the density of urban areas, the proportion and extensiveness of croplands, the existence of some scrub cover and semi-continuous grasslands.
Conclusions This study outlines the influence of the spatial scale and the importance of the sampling bias corrections in HSM, and to our knowledge, it is the

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M. Vergara (✉) · A. Ruiz-González
Department of Zoology and Animal Cell Biology,
University of the Basque Country, UPV/EHU, c/ Paseo de
la Universidad, 7, 01006 Vitoria-Gasteiz, Spain
e-mail: m1v2r3@hotmail.com

M. Vergara · A. Ruiz-González
Systematics, Biogeography and Population Dynamics
Research Group, Lascaray Research Center, University of
the Basque Country, UPV/EHU, Avda. Miguel de
Unamuno, 3, 01006 Vitoria-Gasteiz, Spain

S. A. Cushman
U.S. Forest Service, Rocky Mountain Research Station,
2500 S. Pine Knoll Dr., Flagstaff, AZ 86001, USA

F. Urra
Biodiversity Unit, Environmental Management of Navarre
S.A., c/ Padre Adoain 219 bajo, 31015 Pamplona, Spain

first comparing multiscale habitat selection and niche divergence of two related marten species. This study provides a useful methodological framework for multispecies and multiscale comparatives.

Keywords HSM · Scale dependency · Sampling bias · Niche divergence · Maxent · Pine marten · Stone marten

Introduction

Habitat suitability models (HSM, Girvetz and Greco 2009; Koreň et al. 2011; Bellamy et al. 2013), also referred as species distribution models (SDM, Kramer-Schadt et al. 2013; Syfert et al. 2013; Fourcade et al. 2014) or environmental (or ecological) niche models (ENMs, Warren et al. 2010; Warren and Seifert 2011), have become a fundamental tool in ecology and biogeography as they correlate the presence of species at multiple locations with relevant environmental covariates to estimate habitat preferences and/or predict species distributions (Elith et al. 2011). The identification of the factors constraining species presence is central to identify the most suitable areas for a particular taxa, to infer relative probability of occurrence in areas where no systematic surveys have been conducted (Fourcade et al. 2014), to assess the potential expansion of invasive species (e.g. Elith et al. 2010; Jiménez-Valverde et al. 2011) or to estimate future ranges under different climate change scenarios (e.g. Khanum et al. 2013). HSMs can also be particularly useful to explore the environmental characteristics conditioning several species' overlapping ranges in order to quantitatively estimate the niche divergence in related species and to infer the roles of competitive interaction (e.g. Wellenreuther et al. 2012). This application is particularly interesting as a species' realized niche could be restricted by competition with sympatric congeners (Anderson et al. 2002).

Most species records are only available in the form of presence-only datasets (PO), which provide solid information regarding the species' presence but no direct data regarding absences (Pearson et al. 2007). Thus, in recent decades, there has been an increasing focus on developing methods to work with this information (reviewed in Yackulic et al. 2013). MAXENT (Phillips et al. 2006) is one of the most commonly used HSM techniques dealing with PO data (Elith et al. 2006, 2011; Syfert et al. 2013). All PO based HSM methods work under the assumption that the entire area under study has been systematically and randomly sampled (Elith et al. 2011). Yet, most datasets include spatially biased presence records. Lately, the effect of sampling bias in model performance has increasingly been acknowledged and several correction methods have been proposed to improve model accuracy (Anderson and Gonzalez 2011; Kramer-Schadt et al. 2013; Syfert et al. 2013; Brown 2014). Consequently, Fourcade et al. (2014) recommended evaluating several types of corrections before choosing the final correction method based on (a) their effect in classical model evaluation metrics (e.g. AUC) and (b) the adequacy of the produced habitat suitability map to a priori knowledge of a given species distribution.

To produce a realistic HSM, habitat features must be measured at spatial resolutions that are relevant to the organism being modeled based on its ecological adaptations and life-history strategy, as species use habitats differently at widely divergent scales (Johnson 1980; Cushman and McGarigal 2004; Graf et al. 2005). Even when the correct variables are employed, the incorrect specification of the scale at which scale-dependant characteristics operate could lead to a dramatically different interpretation of which factors are actually influencing the occurrence of a given species (e.g. Thompson and McGarigal 2002; Girvetz and Greco 2009; Bellamy et al. 2013; Shirk et al. 2014). Nevertheless, there is no a priori way to infer the grain and extent at which each environmental predictor is most strongly related to species presence (Shirk et al. 2012). Therefore, habitat suitability modeling has shifted from models based exclusively in expert's opinion to increasingly complex multiscale models to reveal the true grain at which species respond to the landscape. Multiscale HSMs allow more accurate predictions of species occurrence based on the systematic variation of the scale of analysis of each variable to find the dominant scale at which they operate to build the models (e.g. Shirk et al. 2012). In this context, recent studies conducted on mammals (e.g. Wasserman et al. 2012; Bellamy et al. 2013; Mateo-Sánchez et al. 2013; Shirk et al. 2014) have demonstrated the effectiveness of multiscale approaches.

The European pine marten (*Martes martes*) and the stone marten (*Martes foina*) are two closely related mustelids living sympatrically over a wide area of Europe (Proulx et al. 2004), and the northern Iberian Peninsula represents both the southern limit of the pine marten distribution and the southernmost area of sympatry in southwestern Europe (Fig. 1). These species share similar biological characteristics (e.g. body-size, trophic niche or activity patterns) making it challenging to reliably determine differences in distribution based on observational data (Proulx et al. 2004). The application of molecular methods on non-invasively collected faecal samples has proven to be a cost-effective way to reliably verify and monitor these elusive species' presence (e.g. Ruiz-González et al. 2013) and thus, also useful to build PO dataset for HSM purposes.

Recent studies have revealed that the pine marten is not as obligately dependent on forest habitats as previously believed (Virgós et al. 2012) and may be capable of colonizing agricultural landscapes containing highly fragmented woodland and forest patches (Mergey et al. 2011; Balestrieri et al. 2015). However, the pine marten is either threatened or rare in many countries, while the stone marten's geographic range has expanded due to its behavioral plasticity, broader habitat niche and less vulnerability to anthropogenic impacts (Proulx et al. 2004; Goszczyński et al. 2007; Herr et al. 2009). Despite their extensive overlapping range, few studies addressing the differences in the pine and the stone marten habitat associations have been conducted (e.g. Goszczyński et al. 2007; Posłuszny et al. 2007; Larroque et al. 2015) and currently no in-depth studies have been published on their multiscale habitat selection (Virgós et al. 2012).

The goal of this paper is to compare and contrast pine and stone marten multiscale habitat selection in a sympatric area of northern Spain by investigating how different environmental characteristics, measured at varying spatial scales, shape the distribution of each species. Subsequently, we compared the performance of three methods of sampling bias correction (Fourcade et al. 2014) to improve the predictions of the final habitat suitability maps. Finally, the resulting HSMs were compared to explore niche differentiation among the species. To our knowledge, this is the first study comparing multiscale habitat selection of two sympatric marten species to clarify their habitat preferences and niche divergence when coexisting.

Materials and methods

Study area

The study area comprises the regions of the Basque Country and Navarre and the surrounding territories of Cantabria, Castille and Leon and La Rioja (northern Spain, Fig. 1). The area is located in the southern range limit of the pine marten where it occurs sympatrically with the stone marten. The study area is 31,500 km^2 with forest covering 31.3 %, non-

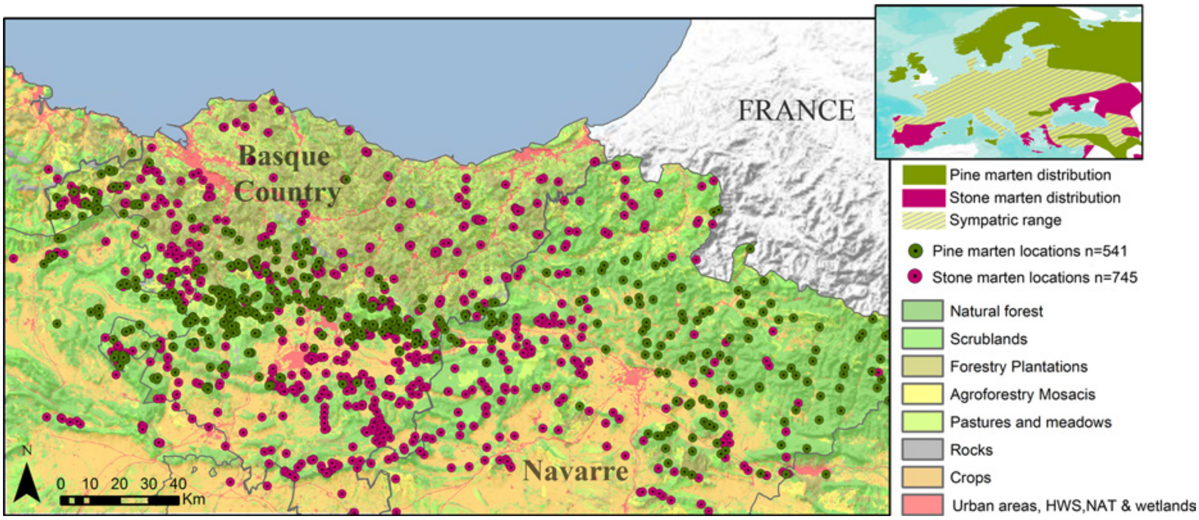


Fig. 1 Map of the study area showing the distribution of the pine and stone marten records used to build the models. Each land cover type is shaded in a *different color*. The *inset* presents the species ranges and overlap in Europe. (Color figure online)

forested mountains 27.3 %, cultivated lands 26.8 % and urban, infrastructure and remaining land cover types 14.6 % of the territory, respectively. Elevation ranges from sea level to 2017 m (Mount Ori, Pyrenees). Three biogeographic regions converge in the area, including Atlantic, Mediterranean and Alpine, roughly corresponding to three sections with varying landscape compositions: the northern Basque Country, mainly covered by forestry plantations and highly fragmented natural forests; the north-eastern Navarre, dominated by continuous natural forest systems; and extensive cultivated lands and urban areas located primarily in the southern areas of both provinces (Fig. 1).

Marten presence data: combining long-term non-invasive genetic sampling and species records from different field data sources

Two main sources of PO data were used in this study to accurately assess the spatial distribution of both species. First, we used faecal sampling to collect non-invasive genetic samples from both species across the study area between 2005 and 2012. Martens and other carnivores use forest roads and frequently defecate on them as a way of visual-scent marking (Birks et al. 2004). Thus, sampling was conducted opportunistically along linear features, such as forest trails and/or rural paths, to increase sampling probability. As *Martes* sp. faeces cannot be distinguished from each other visually and can also be easily confused with those of other carnivores (Davison et al. 2002; Ruiz-González et al. 2008), we applied a mtDNA molecular method that effectively identifies the species (Ruiz-González et al. 2008). Additionally, we included unequivocal species records from road-killed, live-trapped, hair-trapped (confirmed by genetic identification and morphological characteristics of hairs) and/or camera-trapped individuals obtained in the framework of different carnivore surveys funded by regional or national administrations (Spanish Ministry of Environment, Regional Governments of Navarre and Basque Country and Alava and Bizkaia Provincial Councils; Table S1 in Online Appendix). The locations of the genetically identified faeces and those from different sources were combined to build a single PO dataset for each study species (Table S1 in Online Appendix).

Environmental layers

The environmental variable set comprised a total of 40 variables belonging to five categories (Table 1). All variables were resampled to a UTM projection (ETRS89) with a 30 m cell size. Nine land cover types were derived from the land use information obtained in vector format from the Spanish Forest Map at scale 1:50,000 (Spanish Ministry of Agriculture, Food and Environment 2006). FRAGSTATS software v 4.2 (McGarigal et al. 2012) was used to calculate (a) five landscape level metrics characterizing landscape composition, configuration and edge contrast, and (b) four class composition and configuration level metrics (Table 1). Elevation data was obtained from a 25 m resolution Spanish Digital Elevation Model (Spanish Geographical National Institute; CNIG 2008) to calculate the Focal Mean Elevation (ELEV), Compound Topographic Index (CTI) and Roughness (ROUGH) using the Surface Gradient and Geomorphometric Modeling tool (Evans et al. 2014) in ArcGIS v.10.0 (ESRI). The density of highways (HWS), national (NAT) and autonomic roads (AUT), were assessed separately derived from the 1:25,000 scale spatial products developed by CNIG to incorporate the anthropogenic disturbance. To test the influence of temperature in each marten distribution the mean annual temperature (Iberian Climate Atlas; AEMET 2011) was included among the analyzed variables.

Each variable (Table 1) was independently tested at 6 scales using circular windows with radii of 1, 2, 4, 8, 16 and 32 km (i.e. a univariate HSM for each variable/scale combination. See step 1 below). This analysis is multi-scale because it evaluated the relationships between marten occurrence environmental variables across six spatial scales of environmental data. The scales were defined in space, but not time, as we employed nested circular windows applied to a common set of GIS layers derived at the same temporal scale. We chose a range of six spatial scales of focal neighborhood extent (1–32 km) since they span the range of scales that martens can plausibly interact with across their lifetime movements (from within home range habitat use to patterns of population connectivity affected by dispersal), and these ranges of scales have previously been found to explain habitat selection in the pine marten (e.g. Zalewski et al. 2004), the stone marten (Herrmann 1994) and

Table 1 The set of 40 independent variables considered for analysing multiscale martens habitat suitability

Variable type	Metric	Abbreviation
Human pressure	Highways density	HWS
	National road density	NAT
	Autonomic roads density	AUT
Topographic	Focal mean of elevation	ELEV
	Roughness	ROUGH
	Compound Topographic Index	CTI
Climatic	Mean annual temperature	TEMP
Landcover (landscape-level metrics)	Aggregation index	AI
	Contrast-weighted Edge Effect	CWED
	Edge density	ED
	Patch density	PD
	Shannon Diversity Index	SHDI
Landcover (class-level metrics)	Patch density	PD_(Nat, Fp, Ag, Pa, Scr, Cr, Urb)
	Area-weighted mean	AREAam_(Nat, Fp, Ag, Pa, Scr, Cr, Urb)
	Gyrate_am	GYR_(Nat, Fp, Ag, Pa, Scr, Cr, Urb)
	Percentage of landscape	PLAND_(Nat, Fp, Ag, Pa, Scr, Cr, Urb)

Variables are grouped into five categories (Human pressure, topographic, climatic, and landcover landscape-level and class-level metrics). The four class level variables (PD, AREAam, GYR, PLAND were calculated for each of the seven land cover types considered. All layers were produced at six different spatial scales (1, 2, 4, 8, 16 and 32 km) except for HWS, NAT, AUT, ELEV, ROUGH, CTI that were additionally analyzed at high-resolution scale (125, 250 and 500 m)

In landcover class-level metrics: *Nat* natural forest, *Fp* forestry plantations, *Ag* agroforestry mosaics, *Pa* pastures, *Scr* scrublands, *Cr* crops, *Urb* urban areas

other marten species (e.g. Wasserman et al. 2012; Shirk et al. 2014). HWS, NAT, AUT, ELEV, ROUGH and CTI were additionally tested at high-resolution scale (125, 250 and 500 m).Our analysis only varied focal neighborhood extent and not grain of the underlying spatial data. In our analysis we used an empirical optimization using the MAXENT statistical procedure to identify the best scale for each predictor variable.

Marten HSMs

Habitat selection is hierarchical (Johnson 1980) and occurs at multiple spatial scales (Wiens et al. 1987). Our analysis was effectively single-level corresponding roughly to Johnson's (1980) level 2 habitat selection of home ranges within the species range or study area, even though our unit of observation was individual detections rather than home ranges. The critical factor in this regard was our use of the study area as the basis for defining availability.

The main methodological steps followed to build the marten HSMs, and to explore the ecological niche divergence among them, were summarized in a workflow (Fig. 2), while details of the steps are reported bellow.

Step 1: variable pre-selection: bivariate scaling and variable pruning

We conducted an initial bivariate scaling step to test at which scale each variable was most strongly related to the species presence (Fig. 2, Step 1). In this step, each variable (Table 1) at each scale was run independently for each species in MAXENT (Phillips et al. 2006), the most widely used HSM software for predicting species distributions from PO data and a set of environmental variables (Fourcade et al. 2014). MAXENT is a presence-background algorithm that compares occurrence localities with a sample of background pixels to create a prediction of suitability which, according to Elith et al. (2010), produces robust results with sparse, irregularly collected occurrence records, and minimal

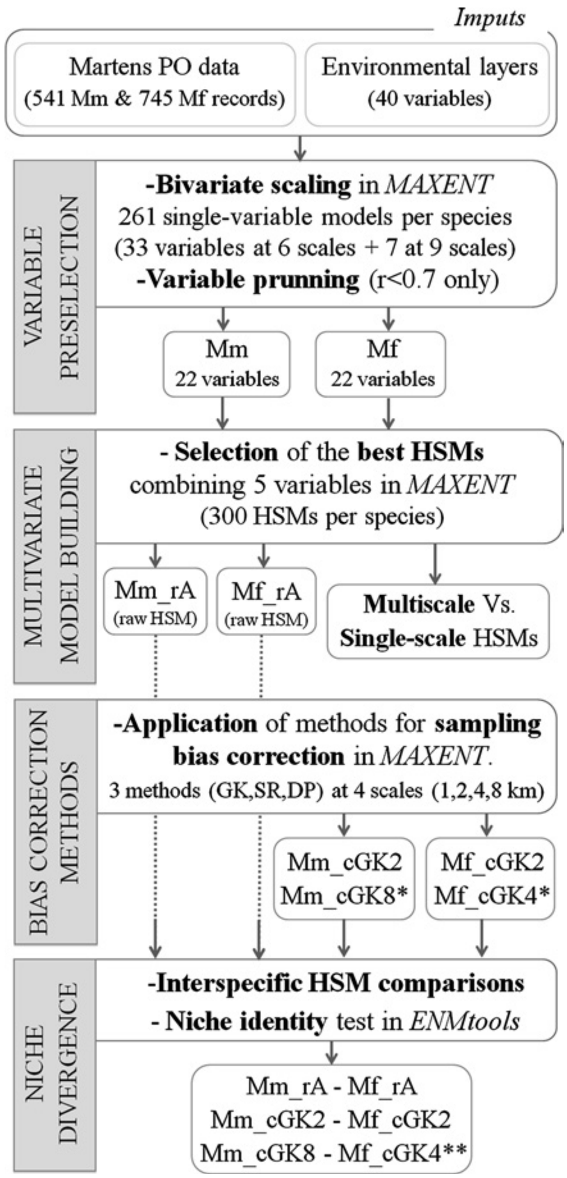


Fig. 2 Study workflow including the input files used and the consecutive steps done to build the HSMs and to test martens' niche divergence. *Optimized HSM for each species. **Optimized model combination

location errors (Elith et al. 2006). Thus, all models were computed in MAXENT v.3.3 using the following parameters as described in Mateo-Sánchez et al. (2013): 20,000 background points, a maximum of 5,000 interactions linear and quadratic functional relations (LQ). We selected LQ only as they prevent locally idiosyncratic responses that can result from incorporating higher-order polynomials, and are easier to interpret from an ecological perspective (Syfert et al. 2013). A random subsample of 75 % of the species occurrence points were used to fit the model ("train") and the remaining 25 % to assess model performance ("test"). We used the AUC values (Area Under the receiver operating characteristic Curve, Fielding and Bell 1997) to compare the performance of the single variable models, selecting the scale at which the variable showed the highest AUC value and discarding the rest (e.g. Mateo-Sánchez et al. 2013). We used AUC (Phillips et al. 2009; Aguirre-Gutiérrez et al. 2013) as the scaling criterion as it is the most commonly used metric for model quality assessment (Kramer-Schadt et al. 2013). MAXENT performs well in the presence of correlated variables; however, it remains desirable to remove highly inter-correlated variables in multivariate analysis to avoid multicollinearity (Mateo-Sánchez et al. 2013). Hence, the candidate set of variables was pruned, discarding the variable (at the best performing scale) with the lowest AUC of each variable pair presenting a Pearson correlation coefficient ≥ 0.7 (Bellamy et al. 2013).

Step 2: multivariate model building

Only those variables remaining after the bivariate scaling and variable pruning steps were included in the multivariate models. 300 HSMs per species were constructed, each containing a different set of five randomly selected predictors (Mateo-Sánchez et al. 2013), including variables belonging exclusively to the same category and combinations of two or more categories (Table 1). The main reason for combinations of sets of five variables was to avoid overfitting by adding spurious variables. Besides, by having all models with the same total number of variables it ensures that they are comparable in terms of number of parameters, which is related to variance explained. Multivariate HSMs, built combining five variables, were run in MAXENT with the same parameters used in the bivariate scaling step.

To evaluate model performance, each species' multivariate models were ranked according to their AUC values while the relative predictive power of each variable was assessed based on the jackknife measure of test AUC. Then, we explored the 10 top performing models for each species (i.e. those showing the highest AUC values) to compare the incidence of the environmental predictors and select the best raw multivariate HSM for each species (models run without any bias correction; i.e. Mm_rA and Mf_rA). Finally, to estimate how the scale optimization affected the predictive performance of the HSMs, we compared the best performing multiscale models (Mm_rA and Mf_rA) with those built with the same variables but measured at each single scale (i.e. 1, 2, 4, 8, 16 and 32 km).

Step 3: sampling bias correction methods

One limitation of HSMs, especially when occurrence localities are derived from opportunistic observations rather than representative surveys, is the presence of sampling bias, where some areas in the landscape (i.e. easily accessible areas, near roads or towns) are sampled more intensively than others (Phillips et al. 2009). This geographic sampling bias can strongly affect the reliability of HSMs when important areas of the environmental space suitable for species are missing, poorly represented, or overrepresented, leading to spurious results and inappropriate management decisions (Kramer-Schadt et al. 2013; Fourcade et al. 2014). When information quantifying sampling effort exists, it can be used to correct for sampling bias. However, in empirical studies this information is often unknown (Fourcade et al. 2014). Thus, we implemented three of the correction methods applied in Fourcade et al. (2014), to address the most plausible sources of sampling bias in our dataset. We used SDM toolbox v.1.1 (Brown 2014) for ArcGIS v.10.0 (ESRI 2014) to: (a) rarefy the species occurrence data (SR); (b) to produce sampling probability maps (GK); and (c) to restrict the background area (DP) at four spatial scales.

(a) *SR* With the aim of eliminating the influence of spatial clusters of localities, the *spatially rarefy occurrence data tool* was used to reduce the locality records to a single point within the specified Euclidian distance. The resulting datasets for each marten, with filtered locations at 1, 2, 4 and 8 km radii, were later used as each species' presence records. Then, we ran MAXENT to produce four HSMs per species combining the spatially rarefied locations and the environmental predictors included in the best HSMs.

(b) *GK* We produced a bias grid that up-weighted PO data points with fewer neighbors in the geographic landscape using the *Gaussian Kernel Density of sampling localities tool*. This sampling probability surface (showing values of 1 to reflect no bias and higher values representing increasing bias) was computed including both marten species' locations to focus on the widespread spatial sampling biases as the probability of detecting either species is, a priori, the same. Each derived Gaussian Kernel map (at 1, 2, 4 and 8 km) was implemented in the bias file option in MAXENT together with the environmental predictors included in each marten best HSMs.

(c) *DP* To prevent using background data from environmental conditions outside the range sampled we used the *sample by distance from observation point tool* which tells MAXENT to sample background points within a maximum buffer size of 1, 2, 4 and 8 km from known occurrences. Each background restriction mask was implemented in the bias file option in MAXENT.

Ten replicates per model (both raw and 12 corrected HSMs per species) were built following a resampling method, randomly selecting a subsample of 25 % of observation records for model validation in each replicate.

To compare and evaluate the corrected HSM's fit, we employed two threshold-independent and one threshold-dependent metrics. First, to assess differences in the general model fit we used the $\mathrm{AUC}_{\mathrm{TEST}}$ which, although criticized (Lobo et al. 2008; Warren and Seifert 2011), is appropriate for comparison of models produced with different settings but for the same species in the same study region, as in this case (Lobo et al. 2008; Anderson and Gonzalez 2011). Then, to quantify overfitting, we employed $\mathrm{AUC}_{\mathrm{DIFF}}$, the difference between AUC values based on training ($\mathrm{AUC}_{\mathrm{TRAIN}}$) and test ($\mathrm{AUC}_{\mathrm{TEST}}$) localities (Warren and Seifert 2011). As a final test of model performance we assessed the spatial patterns of the presences predicted as present and the presences predicted as absent of the HSMs. For this purpose, we chose as probability threshold MAXENT's maximum training sensitivity plus the specificity logistic threshold (MTR), which has been shown to produce accurate predictions (Jiménez-Valverde and Lobo 2007; Svenning et al. 2008). Then, models were converted to binary maps (presence/absence) selecting the MTR of each model as a cut-off, where values above the threshold are predicted as a presence and values below as an absence (Syfert et al. 2013). Additionally, raw and corrected HSMs were visually examined and evaluated based on expert knowledge on the distribution of each species and the habitat types in with they are known to occur to ensure reliability and to identify the best performing final HSMs (e.g. Brown 2014; Radosavljevic and Anderson 2014).

Step 4: marten niche divergence

First, to explore spatial niche separation, we calculated and visually examined the spatial difference between relative probability of occurrence values of the two species' for the different HSMs: (a) raw HSMs, and (b) the corrected HSMs according to two different criteria (i) those outperforming the raw in all aforementioned criteria and, (ii) those HSMs with the lowest percentage of presences predicted as absent (Fig. 2, step 4).

Further, to statistically test if models produced for each species were more different than expected by chance, we computed an identity test in ENMtools v.1.4 (Warren et al. 2008, 2010), for the aforementioned three comparisons, by comparing the observed measure of niche overlap (Schoener's D and Hellinger's I metrics) to a null distribution calculated with 100 replicates, in which the null hypothesis of niche identity is rejected when the empirically observed value is significantly different from the pseudo-replicate data set (Warren et al. 2010).

Results

Marten presence data

From the 972 faecal samples collected, we selected 899 samples that were the freshest and highest quality for genetic analysis. 754 were genetically identified as one of the two marten species (Table S1 in Online Appendix). Thus, unequivocal species identification was possible in 83.87 % of the samples. In the remaining 16.12 %, the DNA extracted was not amplified by the primers used. The results of non-invasive genetic sampling together with the combination of unequivocal species records obtained in the framework of different carnivore surveys ($n = 532$), resulted in a PO dataset with 541 pine marten and 745 stone marten locations to build the HSMs.

Bivariate scaling and variable pruning

The predicted relative habitat suitability, for each environmental variable at each scale and species, revealed high sensitivity of habitat relationships to the scale at which habitat variables were measured (Table S2 in Online Appendix). Comparisons among different scales revealed that most metrics were most strongly related to marten's habitat suitability at broad-scales (16–32 km, 48.75 %), including all three categories of road density and the majority of land-cover class-levels metrics across cover types. A clear difference between the stone and the pine marten was found regarding landcover landscape-level metrics (AI, CWED, ED and PD). While variables measured at broad scale performed best for the pine marten, variables at medium-scales (4–8 km) did better for the stone marten. Patch density (PD) for six of the seven landcover classes (except for patch density of natural forest, PD_Nat) had best performance at fine-scales (1–2 km) in both species. The CTI was the only metric selected at a high-resolution scale (125–500 m). After pruning, 22 variables remained from the initial set of 40, 18 of which were shared by both species at diverse scales and four were unique to each species (Table S2 in Online Appendix).

Performance of multivariate HSMs

Among the 10 best performing multivariate models for each species (Table 2) the HSMs produced for the pine marten showed substantially higher discrimination ability, as measured by AUC ($AUC = 0.818$–0.835) than those for the stone marten ($AUC = 0.720$–0.724). The best predictions of both species' habitat suitability were produced using variables measuring human-pressure (NAT, AUT, HWS), land-cover metrics (SHDI, PLAND_Nat, Scr, Cr, Urb; PD_Fp, Ag, Pa, Cr, Urb; AREAam_Cr) and climatic (TEMP) metrics. Topographic variables (Rough and CTI) were not included in any high-performing models.

Table 2 Ten best performing raw multivariate models for the pine marten (Mm_r) and the stone marten (Mf_r) ranked by AUC values (A–J)

Model	V.CAT	Variables					AUC
Mm_rA	HP, CL, LC	PLAND_Urb 32 km	PLAND_NAT 2 km	TEMP 4 km	Gyr_Ag 32 km	PD_Fp 2 km	0.835
Mm_rB	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 16 km	TEMP 4 km	Gyr_Ag 32 km	PD_Fp 2 km	0.833
Mm_rC	HP, CL, LC	PLAND_Urb 32 km	TEMP 4 km	Gyr_Ag 32 km	PD_Fp 2 km	AUT 8 km	0.832
Mm_rD	HP, CL, LC	PLAND_Urb 32 km	PLAND_NAT 2 km	TEMP 4 km	Gyr_Ag 32 km	AUT 8 km	0.828
Mm_rE	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 16 km	TEMP 4 km	Gyr_Ag 32 km	PD_Pa 1 km	0.828
Mm_rF	HP, CL, LC	PLAND_Urb 32 km	TEMP 4 km	Gyr_Ag 32 km	PD_Fp 2 km	HWS 32 km	0.828
Mm_rG	HP, CL, LC	PLAND_Urb 32 km	PLAND_NAT 2 km	TEMP 4 km	Gyr_Ag 32 km	PD_Urb 2 km	0.826
Mm_rH	HP, CL, LC	PLAND_Urb 32 km	PLAND_NAT 2 km	TEMP 4 km	Gyr_Ag 32 km	PD_Ag 1 km	0.825
Mm_rI	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 16 km	TEMP 4 km	Gyr_Ag 32 km	PD_Cr 1 km	0.825
Mm_rJ	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 16 km	TEMP 4 km	Gyr_Scr 16 km	PD_Fp 2 km	0.818
Mf_rA	HP, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	PLAND_Scr 32 km	AREAam_Cr 32 km	PD_Pa 2 km	0.724
Mf_rB	HP, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	PD_Urb 2 km	PD_Pa 2 km	PLAND_Scr 32 km	0.723
Mf_rC	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	PD_Pa 2 km	PLAND_Scr 32 km	TEMP 16 km	0.723
Mf_rD	HP, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	PD_Urb 2 km	AREAam_Cr 32 km	PLAND_Scr 32 km	0.723
Mf_rE	HP, LC	PLAND_Urb 32 km	NAT 16 km	PD_Pa 2 km	PLAND_Scr 32 km	PLAND_Cr 4 km	0.723
Mf_rF	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	AREAam_Cr 32 km	PD_Pa 2 km	TEMP 16 km	0.722
Mf_rG	HP, LC	PLAND_Urb 32 km	NAT 16 km	PD_Urb 2 km	PLAND_Scr 32 km	PLAND_Cr 4 km	0.721
Mf_rH	HP, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	PD_Pa 2 km	PLAND_Scr 32 km	SHDI 2 km	0.721
Mf_rI	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	PD_Urb 2 km	PLAND_Scr 32 km	TEMP 16 km	0.721
Mf_rJ	HP, CL, LC	PLAND_Urb 32 km	PLAND_Cr 4 km	AREAam_Cr 32 km	PLAND_Scr 32 km	TEMP 16 km	0.720

Variables are ordered according to their relative contribution to the model. The scale at which each predictor showed the best performance is reported immediately after each variable

V.CAT variable categories, *HP* human-pressure, *CL* climate, *LC* landcover

The most important predictor of both species' occurrence was the percentage of urban areas (PLAND_Urb). The density of urban patches (PD_Urb) was also an important predictor. The influence of the human impact was further evidenced by the inclusion of both the percentage and the density of crops patches in all the stone marten models (PLAND_Cr, PD_Cr) and the correlation length of agroforesty mosaics (GYR_Ag) in nine out of 10 pine marten models. Although to a lesser extent, the three types of road density metrics (HWS, AUT and NAT) were also included. The percentage of natural forested areas (PLAND_Nat) and patch density of forestry plantations (PD_Fp) were highly related to pine marten habitat suitability. Temperature was present in each of the pine marten's best performing models, whereas the area covered by scrublands (PLAND_Scr) was associated with the presence of the stone marten.

We found substantial differences in predictive performance between the multiscale HSMs with the highest AUC (Mm_rA and Mf_rA, Table 2) and the corresponding single-scale models at 1, 2, 4, 8, 16 and 32 km (Fig. S1 in Online Appendix). Multiscale models showed higher discrimination ability, as evidenced by larger AUC values. Among the single-scale models, those including all variables measured at 1 km showed the weakest performance in the pine ($AUC_{MM} = 0.790$) and the stone ($AUC_{MF} = 0.653$) marten. The maximum performance for a single scaled model was archived at 8 km for the pine marten ($AUC_{MM} = 0.810$) and at 32 km for the stone marten ($AUC_{MF} = 0.702$), but were weaker than the optimized multiscale HSMs ($AUC_{MM} = 0.835$; $AUC_{MF} = 0.724$, Fig. S1 in Online Appendix).

Bias correction methods in marten HSMs

No correction method (GK, SR, DP) or scale (1, 2, 4, 8 km) ranked best based on the three evaluation criteria (AUC_{TEST}, AUC_{DIFF}, % presences predicted as absent; Table 3) for both martens. For the pine marten, only corrected models run with the Gaussian Kernel bias files (Mm_cGK) presented higher AUC values than the raw model. Mm_cGK and Mm_cDP presented lower overfitting (AUC_{DIFF}), in contrast to what was observed for the Mm_cSR models. Regarding model sensitivity (% of actual presences correctly predicted), the best results were obtained for Mm_cGK and Mm_cSR models, while no Mm_cDP model showed higher values than the raw model. Only Mm_cGK2 outperformed the raw model in all pine marten comparisons, presenting higher AUC, smaller AUC_{DIFF} values and slighter presences predicted as absent rate. Within the stone marten models, only corrections with Mf_cGKs improved the predictive performance and reduced the overfitting. The proportion of presences predicted as absent was reduced in almost all Mf_cDP and Mf_cGK models but not in any Mf_cSR model. Mf_cGK1 and Mf_cGK2 were the only models outperforming the raw model in all comparisons.

The distributions of presences predicted as present (PP) and presences predicted as absent (PA) of (a) raw HSMs (Mm_rA and Mf_rA), (b) corrected HSMs (i) outperforming the raw HSMs in all aforementioned criteria (Mm_cGK2 and Mf_cGK2) and (ii) corrected HSMs with the lowest percentage of PA (Mm_cGK8 and Mf_cGK4) were visually explored (Fig. S2 in Online Appendix). Overall, correcting for geographic sampling bias led to a drop in the actual locations that were predicted as absences (%PA, Table 3) and an increase in the area available for each species (%AREA, Table 3). In the pine marten models, no significant increase in %PA was found in the Basque Country area (Fig. S2 in Online Appendix). In Navarre ($n = 134$), however, PA were reduced by 21.6 % (Mm_cGK2) and 74.7 % (Mm_cGK8). Correcting for sampling bias also resulted in a smaller decease in PA in the stone marten (3.6 %, Mf_cGK2 and 17.8 % Mf_cGK4).

Raw and corrected multiscale HSMs

Three final habitat suitability maps are presented for the pine marten (Fig. 3). The first is the raw Mm_rA, built with PLAND_Urb, PLAND_Nat, Temperature, GYR_Agr and PD_Fp variables at the best performing scale (Table 2) without spatially rarefying occurrence records or applying any bias file. Based on this model, we can clearly distinguish a region of mostly continuous natural forested area and forestry plantations from 800 to 1500 m showing the highest probability of presence for the pine marten. A smaller patch on the west was also identified as an area of elevated probability. The optimal area of the pine marten was well-delimited with the probability decreasing sharply (Fig. 3). The second and third maps correspond to the corrected Mm_cGK2 and Mm_cGK8 models, built using the same variable set, but including a bias file

Table 3 Performance of three correction methods (*DP* distance to points, *GK* Gaussian kernel, *SR* spatial rarefaction at four scales for the pine (Mm_c) and the stone marten (Mf_c)

SP	Model	N	AUC_{TEST}	AUC_{DIFF}	MTS	%PA	%PP	%AREA
Pine marten	Mm_cDP1	541	0.698	0.012	0.4759	34.38	65.62	35.00
	Mm_cDP2	541	0.735	0.013	0.4444	34.01	65.99	31.49
	Mm_cDP4	541	0.770	**0.007**	0.4380	33.83	66.17	24.55
	Mm_cDP8	541	0.798	**0.005**	0.4542	35.49	64.51	20.96
	Mm_cGK1	541	**0.813**	**0.004**	0.4832	32.90	67.10	19.37
	Mm_cGK2	541	**0.807**	**0.004**	0.4937	**29.21**	70.79	24.65
	Mm_cGK4	541	0.801	**0.005**	0.4931	**26.06**	73.94	29.2
	Mm_cGK8	541	0.772	**0.006**	0.4339	**19.22**	80.78	39.32
	Mm_cSR1	322	0.755	**0.011**	0.4447	32.61	67.39	29.54
	Mm_cSR2	241	0.743	0.013	0.4177	**19.92**	80.08	36.55
	Mm_cSR4	138	0.702	0.032	0.3942	**23.19**	76.81	43.26
	Mm_cSR8	62	0.670	0.055	0.4542	33.87	66.13	38.44
	Mm_rA	541	0.804	0.011	0.4234	31.42	68.58	19.04
Stone marten	Mf_cDP1	745	0.586	**0.004**	0.4840	35.03	64.97	53.15
	Mf_cDP2	745	0.601	0.013	0.4546	**22.42**	77.58	60.09
	Mf_cDP4	745	0.645	0.022	0.4372	**23.89**	76.11	50.06
	Mf_cDP8	745	0.706	**0.005**	0.4324	**23.76**	76.24	43.61
	Mf_cGK1	745	**0.722**	**0.002**	0.4517	**23.36**	76.64	39.84
	Mf_cGK2	745	**0.720**	**0.008**	0.4700	**24.70**	75.30	42.67
	Mf_cGK4	745	0.682	0.022	0.4879	**21.07**	78.93	45.90
	Mf_cGK8	745	0.641	0.011	0.4922	30.60	69.40	47.01
	Mf_cSR1	466	0.694	**0.003**	0.4502	30.47	69.53	40.37
	Mf_cSR2	355	0.663	0.012	0.4551	28.45	71.55	44.39
	Mf_cSR4	232	0.652	0.014	0.4595	33.19	66.81	44.57
	Mf_cSR8	99	0.583	0.081	0.4909	49.49	50.51	36.37
	Mf_rA	745	0.718	0.009	0.4294	25.64	74.36	38.77

"SP" refers to the species, "N" to the number of samples included in the model and "MTRS" to the Maximum training sensitivity plus specificity logistic threshold from MAXENT, "%PA" to the percentage of presences predicted as absent, "%PP" to the percentage of presences predicted as present and "%AREA" to the percentage of area above the threshold. (e.g. Mm_cDP1 refers to the corrected HSM for the pine marten using distance to points method at 1 km scale). Values outperforming those for the raw models are reported in bold

with sampling probabilities based on Gaussian Kernels at 2 and 8 km, respectively. Accounting for sampling bias resulted in an increase in the percentage of optimum area available for the species (Mm_cGK2: 24.65 %; Mm_cGK8: 39.32 %) and a homogenization of the differences in probability. This resulted in the recognition of the Pyrenean range (near the French border) as a very suitable area for the pine marten, accurately reflecting the known pattern of occurrence. Thus, the Mm_cGK8 model was selected as the optimal pine marten HSM due to its more realistic predictions.

Stone marten HSMs showed, on average, lower predictive performance than the pine marten and no areas of AUC > 0.8 were identified (Table 3). Stone marten models were built with PLAND_Urb, PLAND_Cr, PLAND_Bus, AREAam_Cr and PD_Pa variables at the best performing scale. Habitat suitability values decreased gradually showing a wide gradient from very optimal (0.7–0.8) to optimal (0.5–0.7) and suboptimal conditions (<0.35). Although to a lesser extent, accounting for sampling bias also resulted in an increase in the suitable range for the stone marten (Table 3). As a result, based on the Mf_cGK4 model, the species could be more likely found in an extensive and continuous central region (Basque Country and north-western Navarre). Only few localities bordering the study extent are predicted to be non-suitable for the stone marten. The Mf_cGK4 model, which presented the lowest PA rate and which showed the highest consistency with existing knowledge of the stone marten distribution, was selected as the stone marten optimized HSM.

Environmental predictors of marten's occurrence

Based on the top performing corrected HSM for the pine marten (Mm_cGK8) the most important variable (31.2 % contribution) was the proportion of the landscape covered by urban areas measured at 32 km, showing a unimodal relationship peaking at 13 % cover by urban land uses (Fig. 4). Other important predictors were the percentage of natural forests and temperature (26.1 and 20.3 %, respectively). Relative probability of occurrence increased until the area occupied by natural forest reached its maximum (100 %, based on an area with a radius of 2 km) revealing a clear preference for this cover type. The temperature curve showed the opposite, depicting a dramatic drop in probability of occurrence as temperature rose. GYR_Agr provided a measure of landscape continuity of the agroforestry mosaics, and was positively correlated to the species presence at fine scales (200–800 m) and contributed 18.6 % to the model. The contribution of the patch density of

Fig. 4 Response curves as estimated from MAXENT showing ▶ log response of each marten to five environmental predictors. Probability of presence (logistic output) is shown on the y-axis while the range of the environmental predictor is shown in the x-axis. To prevent that the interaction of variables affect the relationship modeled, the response curves are based on univariate models. Mean response of the 10 replicates is shown in *red* while the standard deviation is shaded in *blue*. (Color figure online)

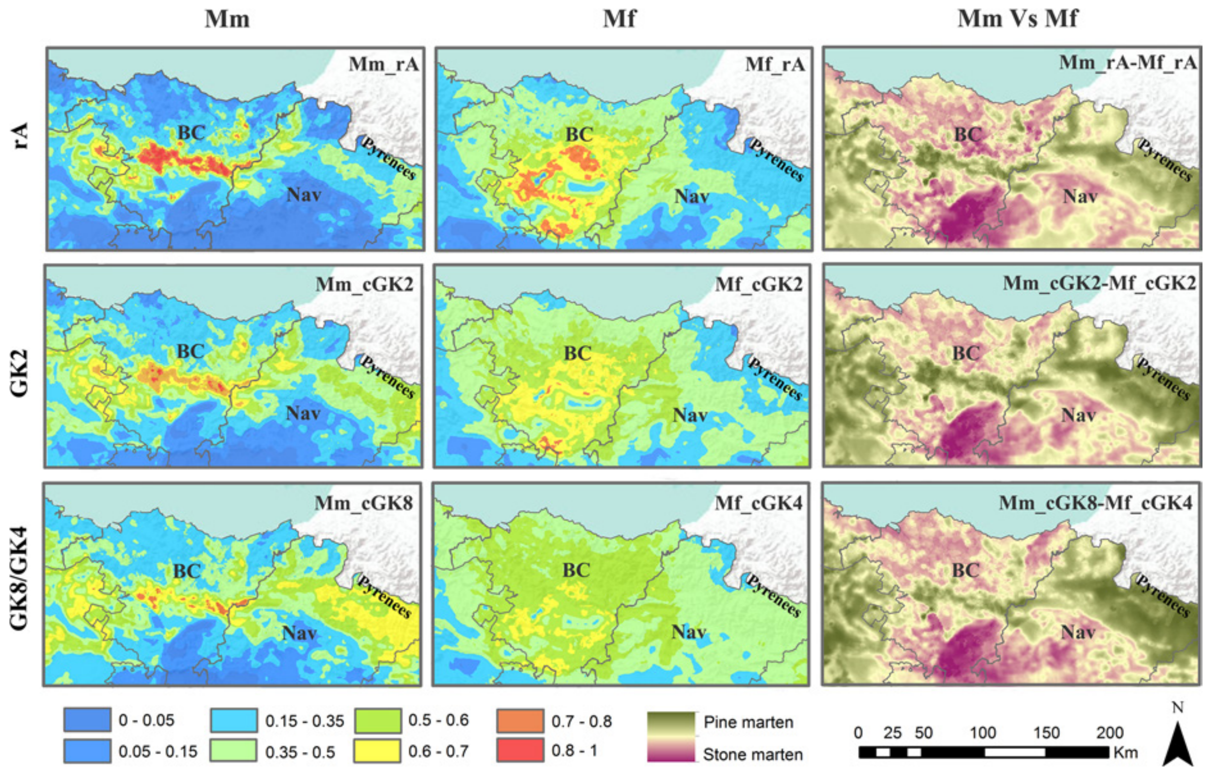
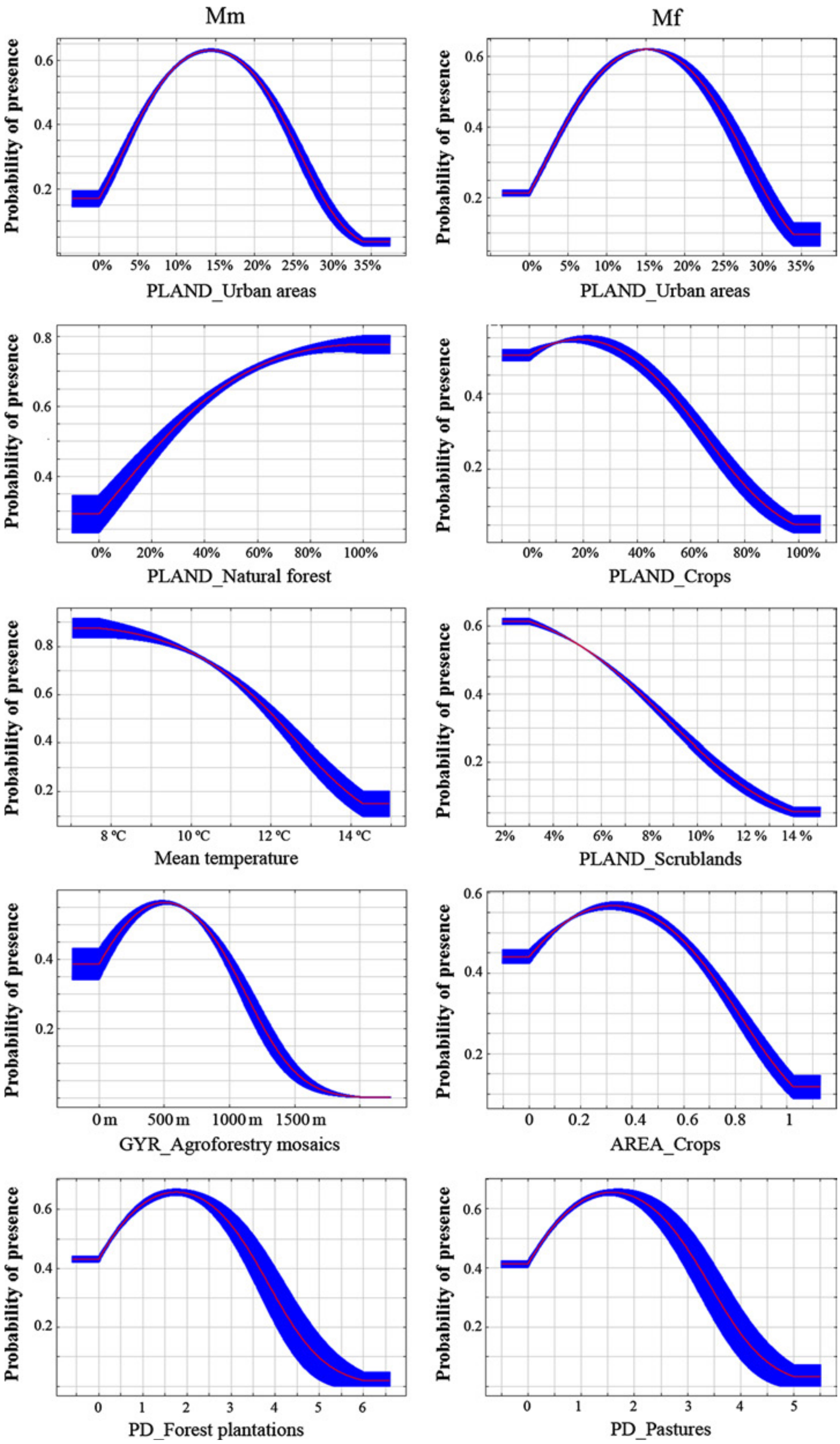


Fig. 3 Habitat suitability maps produced by MAXENT for the pine and the stone marten for three model combinations (raw models: Mm_rA-Mf_rA, and corrected models: Mm_cGK2-Mf_cGK2 and Mm_cGK8-Mf_cGK4) averaged across 10 replicates. The Mm–Mf comparisons display the relative probability of each marten presence calculated from the subtraction of the stone marten probability of occurrence to the corresponding pine marten's model. These maps are represented in a gradient from the maximum probability for the pine marten (in *green*) to the maximum probability for the stone marten presence (in *purple*). (Color figure online)


Mm
Mf
Probability of presence
0.2
0.4
0.6
0% 5% 10% 15% 20% 25% 30% 35%
PLAND_Urban areas
PLAND_Urban areas
0.8
0% 20% 40% 60% 80% 100%
PLAND_Natural forest
PLAND_Crops
8 °C 10 °C 12 °C 14 °C
Mean temperature
2% 4% 6% 8% 10% 12 % 14 %
PLAND_Scrublands
0 m 500 m 1000 m 1500 m
GYR_Agroforestry mosaics
0 0.2 0.4 0.6 0.8 1
AREA_Crops
0 1 2 3 4 5 6
PD_Forest plantations
0 1 2 3 4 5
PD_Pastures

forestry plantations (PD_Fp) at wide scale (32 km) was slight (3.8 %) but positively related to the pine marten occurrence up to intermediate values.

The most important variable (contribution of 39.2 %) in the best corrected HSM for the stone marten, (i.e. Mf_GK4), was the percentage of landscape covered by urban areas measured at 32 km, with the response curve showing suitable areas between 7 and 24 % and with maximum probability at 15 % (Fig. 4). The second variable in terms of importance (18.6 %) was the percentage of crops at 4 km (PLAND_Cr) with probability maximal at 20 %. The stone marten was more likely to be found in areas with a very low density of scrublands (<6 %; PLAND_Scr) and in areas dominated by moderately large cropland patches (with an optimum size around 0.035 km^2; AREAam_Cr) both at the broadest scale evaluated (32 km; Fig. 4). Stone marten occurrence was additionally influenced (7.5 %) by the patch density of pastures (PD_Pa), with relative probability of occurrence decreasing as the density of pasture patches increased at fine-scale (2 km).

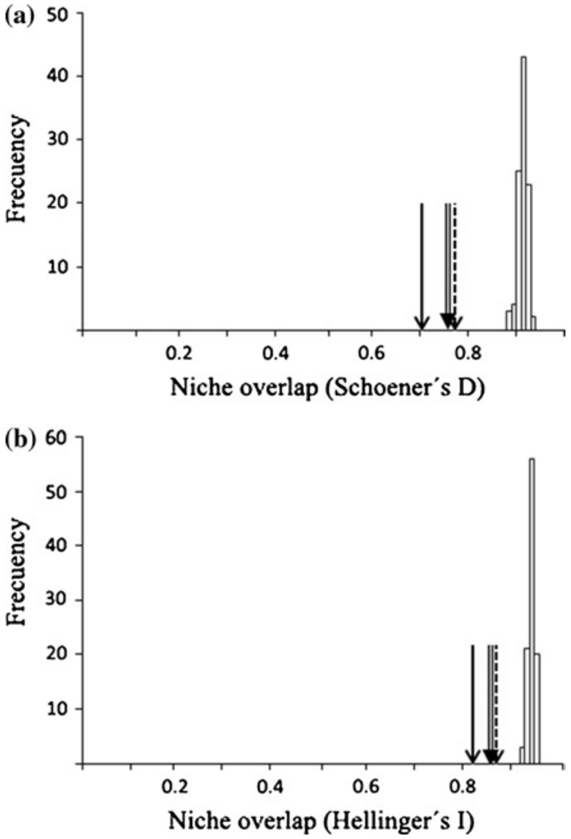


Fig. 5 Result for the niche identity test according to **a** Schoener's D metric. **b** Hellinger's I metric. Martens measured niche overlap between species for the Mm_rA-Mf_rA, Mm_cGK2-Mf_cGK2 and Mm_cGK4-Mf_cGK8 HSMs combinations are reported with a *simple*, *double* and a *dashed arrow* respectively while the *histogram* in white illustrates the distribution of overlaps from the pseudoreplicates

Marten niche divergence

The spatial differences in the relative probability of occurrence values for the two species revealed their divergence in habitat selection (Fig. 3). All three comparative maps revealed similar patterns, with the greener areas indicating a higher probability of finding pine martens than stone martens, and declining gradually with the growth in the likelihood of stone marten presence, shown in purple (Fig. 3). The pine marten occurrence is predicted to be concentrated in the forests and scrublands of the western part of the study area, in the large and continuous natural forested area of northern Navarre and in the forested mountain ranges along the Cantabric-Mediterranean watershed boundary. On the other hand, the stone marten primarily selects the forestry plantations and valleys in the northern Basque Country and the extensive croplands in the south. The species was also found close to the cities where the probability of the pine marten was negligible. However, the stone marten is the only marten recorded in the natural forested areas of the more temperate southern region.

The Identity test further highlighted that the pine and stone marten niches were significantly different ($p < 0.01$) as indicated by the disparity between the null distribution (Fig. 5) and niche overlap values of both metrics observed for the comparative of the optimized HSMs (Mm_cGK8-Mf_cGK4; $D = 0.786$ and $I = 0.859$). The niche dissimilarity between martens was also detected for the Mm_rA-Mf_rA ($D = 0.709$ and $I = 0.809$) and Mm_cGK2-Mf_cGK2 ($D = 0.770$ and $I = 0.851$; Fig. 5) combinations.

Discussion

Effect of scale in marten's habitat selection

Habitat selection of both pine and stone marten were determined by habitat predictors at divergent spatial scales. Fisher et al. (2013) found that the spatial scale of habitat selection of a species was related to body size in 12 terrestrial mammals. The bigger the species, the larger the distance at which an animal would perceive landscape elements (i.e. its perceptual range). In this study, each of the evaluated scales (1–32 km) was represented among the most predictive variable/scale combination. Most variables were selected at 32 km (32.5 %), indicating that martens respond to most landscape features at larger scales than predicted based on body size alone.

Interestingly, road density metrics (evaluated at 9 scales) improved their predictive performance at medium and high scales (8–32 km) despite what could have been expected if the inclusion of road casualties was biasing the predictive performance of the species HSMs. The strongest predictor for both species (PLAND_Urban) showed a very similar response (13–15 %), a result that has to be carefully interpreted. Using circular windows of 32 km, most of the territory holds similar percentages of urban areas due to the heterogeneous configuration of the territory, with a number of scattered small villages and isolated houses and barns spread across the area. Thus, the similar values obtained in both mustelids are explained by the high availability of urban habitats at the explored scale.

The multiscale approach outperformed the single-scale multivariate HSMs for both species, further supporting the scale dependence of the pine and stone marten habitat selection and corroborating previous studies conducted on martens (*Martes* spp. Bissonette and Broekhuizen 1995; *Martes americana*, Shirk et al. 2012, 2014; Wasserman et al. 2012) and other mammals, such as the brown bear (*Ursus arctos*, Mateo-Sánchez et al. 2013) and several bat species (Bellamy et al. 2013).

Environmental predictors shaping marten's occurrence

The optimized HSM for the pine marten (i.e. MmcGK8), which showed that the species was positively associated with cooler areas with a small degree of human disturbance, a high proportion of natural forests, well-connected forestry plantations and medium-extent of agroforesty mosaics, is highly consistent with ecological knowledge about the species. For example, forested habitats are key features for all *Martes* species (Buskirk and Powell 1994; Zalewski and Włodzimierz 2006). Forest offer the best combination of abundant food resources, low risk of predation and well insulated denning sites (reviewed in Virgós et al. 2012). In a recent study conducted in Italy, the distribution and density of pine marten scats (confirmed by DNA analysis) revealed their preference for woodlands (Balestrieri et al. 2015) while its abundance was found to be related to the structure and degree of fragmentation of residual woods.

In our study, as expected, both the percentage of natural forests (PLAND_Nat) and the presence of continuous forestry plantations (PD_Fp) were among the best predictors of the pine marten occurrence. The species was closely associated with natural forests, selecting the best preserved and connected mountainous forested regions. Brainerd and Rolstad (2002) found that forest structure was a more important determinant of the pine marten habitat selection than forest composition and age. Concordantly, presence was also related to connectivity between woodlands (in this case, composed by plantation forests), with relative probability of occurrence higher in unbroken patches than in fragmented forestry landscapes.

The pine marten has been persistently considered to be a forest specialist. Yet, recent studies indicate greater habitat flexibility, and it has been found in agricultural and fragmented landscapes (Balestrieri et al. 2010; Mergey et al. 2012; Virgós et al. 2012; Ruiz-González et al. 2014; Balestrieri et al. 2015). In this study, the extent of agroforestry mosaics was among the variables most related to the species' occurrence. This finding is in agreement with Ruiz-González et al. (2014) where, in addition to woodlands, pine marten gene flow was facilitated by agroforestry mosaics, which represent a transition from forest to agriculture. One possible explanation is that, in fragmented landscapes of temperate regions, the diversity of a wide range of habitat patches promotes higher diversity of food resources than continuous forests (Rosalino and Santos-Reis 2009). This "habitat-diversity" hypothesis has been shown to be related to elevated bird species diversity in moderately fragmented landscapes (e.g. Cushman and McGarigal 2004).

The optimized HSM for the stone marten (i.e. Mf_cGK4) clearly showed that the species' presence was conditioned by the density of urban areas, the proportion and extensiveness of croplands, the existence of some scrub cover and the availability of semi-continuous grasslands. In a recent study, the stone marten was more often detected in rural areas (74.8 %) than in forested habitats (25.2 %; Santos and Santos-Reis 2010). We also found a tendency of the species to select human associated environments, mostly extensive agricultural areas with a high density of villages. However, in the Iberian Peninsula the stone marten is not as synanthropic (Delibes 1983; Santos and Santos-Reis 2010) as in other parts of Europe (e.g. Germany, Luxemburg or Poland), where it is very common in suburban and urban areas, often denning and resting in buildings and barns and causing damage to roofs, insulation and car engines (Proulx et al. 2004; Tikhonov et al. 2008; Herr et al. 2009). The less synantropic behavior of the Iberian stone marten was observed by the greater influence of the density of urban areas at the highest scale (32 km) that at the lowers, as expected in a more urban-associated carnivore. In addition to urban environments, medium-sized croplands and small scattered pastures together with some shrub cover, which provide food, shelter and areas of lower predation risk (Buskirk and Powell 1994; Herrmann 1994), were the main determinants of stone marten habitat selection. Thus, its presence was better explained by the simultaneous use of different human dominated landcover types. This result is in concordance with those reported by Barrientos and Virgós (2006) and Santos and Santos-Reis (2010), where individuals followed a complementation/supplementation strategy with a temporal segregation of food resources, corroborating the importance of mosaic habitats for stone martens compared to strict forest habitats (Virgós et al. 2000; Virgós and García 2002; Santos and Santos-Reis 2010).

Importance of bias correction methods in HSMs building

All datasets derived from opportunistic samplings are likely to suffer from geographic bias, which can strongly affect the predictive performance of the HSMs (Fourcade et al. 2014). In addition, when dealing with common and widespread species, observations are frequently under-reported (Fourcade et al. 2014). However, such data are often the only data available for many species, and must be used with caution, employing the most appropriate sampling bias correction.

To date, no consensus exists regarding the most appropriate metrics and thresholds for selecting from a candidate set of models (Lobo et al. 2008; Warren and Seifert 2011; Kramer-Schadt et al. 2013). In the raw HSMs, the areas predicted as the most suitable for each species tightly matched those with the highest density of species records, indicating effects of sampling bias. The application of GKs reduced overfitting due to the clumped locations, increased the AUC, halved the PA in the pine marten HSMs, decreased error rates up to 20 % in the stone marten, and improved the predictions of the raw models in the Pyrenean region (NE Navarre), tightly matching the areas where the pine marten has been documented to occur. Thus, GKs led to the most realistic potential ranges for these mustelids based on the knowledge of their distribution and the climatic and landcover variables in the area.

Unexpectedly, SR, identified as the most effective sampling bias correction method in recent papers (Kramer-Schadt et al. 2013; Boria et al. 2014; Fourcade et al. 2014), performed poorly across all criteria and spatial resolutions and, in most cases, produced poorer HSMs than the raw ones. DP corrections were also among the less efficient correction methods, in congruence to results reported by Fourcade et al. (2014). Based on the evidence, we strongly recommend evaluating several correction methods and choosing the one that suits each particular species, sampling scheme and objective best.

Niche divergence in sympatric martens

Even if both mustelids are widespread through the area and can coexist locally in some forested regions, the optimized intraspecific HSM comparison (Mm_cGK8-Mf_cGK4) showed well-delimited distribution patterns and a clear spatial segregation and niche divergence, which was further supported by the results of the niche identity test. Several factors are known to affect the niche segregation among martens enabling coexistence, such as differences in habitat selection, diet, thermoregulation and competitive interactions (Goszczyński et al. 2007; Posłuszny et al. 2007; Virgós et al. 2012; Larroque et al. 2015; Wereszczuk and Zalewski 2015). In agreement with previous studies (Delibes 1983; Rosellini et al. 2008; Ruiz-González et al. 2008, 2015) we observed that the pine marten in northern Spain was most frequently found in forested landscapes whereas the stone marten was often associated with agricultural and suburban landscapes, showing clear niche segregation. The observed pattern could be a product of the interspecific competition among martens, favoring the slightly bigger pine marten, with the stone marten occupying higher quality forests when pine marten is absent and expressing niche displacement away from preferred pine marten habitats when co-occurring (Delibes 1983; Virgós and García 2002; Virgós et al. 2012).

The smaller extent of high probability areas of the pine marten occurrence could be s a consequence of both the direct persecution during recent decades and the increasing effects of forest fragmentation and loss (López-Martín 2007; Ruiz-González et al. 2015). The stone marten, which shows a greater behavioral plasticity, would likely have colonized areas previously inhabited by the pine marten, increasing the isolation of its subpopulations (Ruiz-González et al. 2015).

In this study, conducted on the south-western edge of a Eurosiberian species range, temperature played an important role in driving pine marten distribution, which showed a clear preference for cooler and higher elevation environments. The pine marten, which occurs further north, is morphologically better adapted to harsh winters with hairy feet and a denser fur than the stone marten (Wereszczuk and Zalewski 2015). Hence, temperature can be considered a limiting factor determining the southwesternmost pine marten distribution across the area, constraining the species southward expansion and shaping the differences in habitat selection of the two species. The stone marten, however, is less influenced by temperature and could find suitable habitats across the whole temperature range of the study area. Consequently, the actual distribution of the pine marten is likely to be further reduced under a climate change scenario, while an increase in temperature could benefit the more thermophilic stone marten.

In this study we described how these species can co-occur in certain areas but how each species is influenced by a different set of variables explaining their distribution. A comparison conducted in central Poland showed how these closely related species can coexist by differentiating in the use of three-dimensional space in forests and their response to open areas and transformed habitats (Goszczyński et al. 2007). A telemetry based study revealed how the species differed in resting patterns (pine martens rested almost exclusively in forest while stone martens rested in open zones in the proximity of urban areas) and thus in habitat use, which enables coexistence in the same macrohabitat (Larroque et al. 2015). Additionally, Wereszczuk and Zalewski (2015) found that the pine and stone marten utilized different habitats in central Europe and almost completely separated their habitat niches. Certainly, the fine resolution (pixel size) of the environmental variables employed was essential to explore the preferences of each marten species in a landscape of highly intermixed small patches, and to detect the significant niche divergence found among martens that otherwise may remain unknown. Overall, the spatial niche segregation between pine and stone marten described in this work seems to facilitate the pine and the stone marten coexistence in the Iberian Peninsula.

Conclusions

Our results emphasize the importance of analyses conducted at appropriate spatial scales, providing additional support for the need of HSM that account for the scale at which each environmental characteristic is measured. In addition, the incorporation of the Gaussian Kernel method for sampling bias correction led to a robust prediction of each species distribution, and was more accurate than raw models and the two alternative bias correction methods. Based on these results we recommend that all PO based HSMs should account for sampling bias.

Overall, the pine marten was positively associated with cooler areas with a small degree of human disturbance, a high proportion of natural forests, well-connected forestry plantations and medium-extent of agroforesty mosaics. On the other hand, the stone marten presence was conditioned by the density of urban areas, the proportion and extensiveness of croplands, the existence of some scrub cover and the availability of semi-continuous grasslands.

The high resolution sampling grain selected resulted in the inclusion of small but important landscape elements and patches, particularly decisive in a fragmented and heterogeneous area, which allowed the detection of the significant niche divergence found in the closely related marten species co-occurring in northern Spain. To our knowledge, this is the first study comparing multiscale habitat selection and niche divergence of two related marten species. Further, this study provides a useful methodological framework for multispecies and multiscale comparisons.

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References

AEMET (2011) Atlas Climático Ibérico/Iberian Climate Atlas. Agencia Estatal de Meteorología, Ministerio de Medio Ambiente, Rural y Marino, Madrid e Instituto de Meteorologia de Portugal, Lisboa

Aguirre-Gutiérrez J, Carvalheiro LG, Polce C, Emiel van Loon E, Raer N, Reemer M, Biesmeijer JC (2013) Fit-for-purpose: species distribution model performance depends on evaluation criteria—Dutch Hoverflies as a case study. PLoS ONE. doi:10.1371/journal.pone.0063708

Anderson RP, Gonzalez I (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. Ecol Model 222:2796–2811

Anderson R, Peterson A, Gomez-Laverde M (2002) Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 98:3–16

Balestrieri A, Remonti L, Ruiz-González A, Vergara M, Capelli E, Gómez-Moliner BJ, Prigioni C (2010) Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). Acta Theriol 56:199–207

Balestrieri A, Remonti L, Ruiz-González A, Zenato M, Gazzola A, Vergara M, Detorri EE, Saino N, Capelli E, Gómez-Moliner BJ, Guidali F, Prigioni C (2015) Distribution and habitat use by pine marten *Martes martes* in a riparian corridor crossing intensively cultivated lowlands. Ecol Res 30:153–162

Barrientos R, Virgós E (2006) Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. Acta Oecol 30:107–116

Bellamy C, Scott C, Altringham J (2013) Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. J Appl Ecol 50:892–901

Birks JDS, Messenger JE, Braithwaite TC, Davison A, Brookes RC, Strachan C (2004) Are scat surveys a reliable method for assessing distribution and population status of pine martens? In: Harrison DJ, Fuller AK, Proulx G (eds) Martens and fishers (*Martes*) in human-altered landscapes: an international perspective. Springer, New York, pp 235–252

Bissonette J, Broekhuizen S (1995) *Martes* populations as indicators of habitat spatial patterns: the need for a multi-scale approach. In: Lidicker WZJ (ed) Landscape approaches in mammalian ecology and conservation. University of Minnesota Press, Minneapolis, pp 95–121

Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol Model 275:73–77

Brainerd S, Rolstad J (2002) Habitat selection by Eurasian pine martens *Martes martes* in managed forests of southern boreal Scandinavia. Wildl Biol 8:289–297

Brown JL (2014) SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol 5:694–700

Buskirk S, Powell RA (1994) Habitat ecology of fishers and American martens. In: Buskirk S, Harestad A, Raphael M, Powell R (eds) Martens, sables, fish: Biological conservation. Cornell University Press, Ithaca, pp 283–296

Cushman SA, McGarigal K (2004) Patterns in the species–environment relationship depend on both scale and choice of response variables. Oikos 105:117–124

Davison A, Birks JDS, Brookes RC, Braithwaite T, Messenger JE (2002) On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. J Zool 257:141–143

Delibes M (1983) Interspecific competition and the habitat of the stone marten *Martes foina* (Erxleben 1777) in Europe. Acta Zool Fenn 174:229–231

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMcC, Peterson AT, Phillips SJ, Richardson KS, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species’ distributions from occurrence data. Ecography 29:129–151

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57

ESRI (2014) ArcGIS. Environmental Systems Research Incorporated, Redlands, CA

Evans J, Oakleaf J, Cushman S, Theobald D (2014) An ArcGIS Toolbox for surface gradient and geomorphometric modeling, Version 2.0-0

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

Fisher JT, Anholt B, Bradbury S, Wheatley M, Volpe JP (2013) Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes. Ecography (Cop) 36:240–248

Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE 9:1–13

Girvetz EH, Greco SE (2009) Multi-scale predictive habitat suitability modeling based on hierarchically delineated patches: an example for yellow-billed cuckoos nesting in riparian forests, California, USA. Landscape Ecol 24:1315–1329

Goszczyński J, Posłuszny M, Pilot M, Gralak B (2007) Patterns of winter locomotion and foraging in two sympatric marten species: *Martes martes* and *Martes foina*. Can J Zool 85:239–249

Graf RF, Bollmann K, Suter W, Bugmann H (2005) The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. Landscape Ecol 20:703–717

Herr J, Schley L, Roper TJ (2009) Socio-spatial organization of urban stone martens. J Zool 277:54–62

Herrmann M (1994) Habitat use and spatial organization by the stone marten. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) Martens, sables and fishers. Cornell University Press, Ithaca, pp 283–296

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

Jiménez-Valverde A, Peterson A, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biol Invasions 13:2785–2797

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Khanum R, Mumtaz AS, Kumar S (2013) Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modeling. Acta Oecol 49:23–31

Koreň M, Find'o S, Skuban M, Kajba M (2011) Habitat suitability modelling from non-point data. Ecol Inform 6:296–302

Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. Divers Distrib 19:1366–1379

Larroque J, Ruette S, Vandel J-M, Devillard S (2015) Where to sleep in a rural landscape? A comparative study of resting sites pattern in two syntopic *Martes* species. Ecography. doi:10.1111/ecog.01133

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145–151

López-Martín J (2007) *Martes martes* (Linnaeus, 1758). In: Palomo LJ, Gisbert J, Blanco J (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General de Biodiversidad-SECEM-SECEMU, Madrid, pp 302–304

Mateo-Sánchez M, Cushman S, Saura S (2013) 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 1:1–16

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer Software Programs Products by authors Univ. Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html

Mergey M, Helder R, Roeder J-J (2011) Effect of forest fragmentation on space use patterns in the European pine marten (*Martes martes*). J Mammal 92:328–335

Mergey M, Larroque J, Ruette S, Vandel JM, Helder R, Queney G, Devillard S (2012) Linking habitat characteristics with genetic diversity of the European pine marten (*Martes martes*) in France. Eur J Wildl Res 58(6):909–922

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick JR, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19:181–197

Posłuszny M, Pilot M, Goszczyński J, Gralak B (2007) Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces. Ann Zool Fenn 44:269–284

Proulx G, Aubry K, Birks J, Buskirk S, Fortin C, Frost H, Krohn W, Mayo L, Monakhov V, Payer D, Saeki M, Santos-Reis M, Weir R, Zielinski W (2004) World distribution and status of the genus *Martes* in 2000. In: Harrison DJ, Fuller AK, Proulx G (eds) Martens and fishers (*Martes*) in human-altered landscapes: an international perspective. Springer, New York, pp 21–76

Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. J Biogeogr 41:629–643

Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean Europe. Mamm Rev 39:67–78

Rosellini S, Osorio E, Ruiz-González A, Piñeiro A, Barja I (2008) Monitoring the small-scale distribution of sympatric European pine martens (*Martes martes*) and stone martens (*Martes foina*): a multievidence approach using faecal DNA analysis and camera-traps. Wildl Res 35:434–440

Ruiz-González A, Rubines J, Berdion O, Gomez-Moliner BJ (2008) A non-invasive genetic method to identify the sympatric mustelids pine marten (*Martes martes*) and stone marten (*Martes foina*): preliminary distribution survey on the northern Iberian Peninsula. Eur J Wildl Res 54:253–261

Ruiz-González A, Jose Madeira M, Randi E, Urra F, Gómez-Moliner BJ (2013) Non-invasive genetic sampling of sympatric marten species (*Martes martes* and *Martes foina*): assessing species and individual identification success rates on faecal DNA genotyping. Eur J Wildl Res 59:371–386

Ruiz-González A, Gurrutxaga M, Cushman SA, Randi E, Gómez-Moliner BJ (2014) Landscape genetics for the empirical assessment of resistance surfaces: the European pine marten (*Martes martes*) as a target-species of a regional ecological network. PLoS ONE 9:19

Ruiz-González A, Cushman SA, Madeira MJ, Etore R, Gómez-Moliner BJ (2015) Isolation by distance, resistance and/or clusters? Lessons learned from a forest-dwelling carnivore inhabiting a heterogeneous landscape. Mol Ecol 24:5110–5129

Santos MJ, Santos-Reis M (2010) Stone marten (*Martes foina*) habitat in a Mediterranean ecosystem: effects of scale, sex, and interspecific interactions. Eur J Wildl Res 56:275–286

Shirk AJ, Wasserman TN, Cushman SA, Raphael MG (2012) Scale dependency of American marten (*Martes americana*) habitat relationships. In: Aubry KB, Zielinski WJ, Proulx G, Buskirk SW (eds) Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, New York, pp 269–283

Shirk AJ, Raphael MG, Cushman SA (2014) Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). Ecol Appl 24:1434–1444

Spanish Geographical National Institute (CNIG) (2008) Spanish digital elevation model. 250m resolution

Spanish Ministry of Agriculture, Food and Environment (2006) Spanish forest map. 1:50,000

Svenning JC, Normand S, Kageyama M (2008) Glacial refugia of temperate trees in Europe: insights from species distribution modelling. J Ecol 96:1117–1127

Syfert MM, Smith MJ, Coomes DA (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. PLoS ONE. doi:10.1371/journal.pone.0055158

Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landscape Ecol 17:569–586

Tikhonov A, Cavallini P, Maran T, Krantz A, Herrero J, Giannatos G, Stubbe M, Libois R, Fernandes M, Yonzon P, Choudhury A, Abramov A, Wozencraft C (2008) *Martes foina*. The IUCN Red List of Threatened Species, Version 2014.3

Virgós E, García FJ (2002) Patch occupancy by stone martens *Martes foina* in fragmented landscapes of central Spain: the role of fragment size, isolation and habitat structure. Acta Oecol 23:231–237

Virgós E, Recio M, Cortés Y (2000) Stone marten (*Martes foina*) use of different landscape types in the mountains of central Spain. Z Säugetierkd 65:375–379

Virgós E, Zalewski A, Rosalino L, Mergey M (2012) Habitat ecology of genus *Martes* in Europe: a review of the evidences. In: Aubry KB, Zielinski WJ, Proulx G, Buskirk SW (eds) Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, New York, pp 255–266

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol Appl 21:335–342

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883

Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 1:607–611

Wasserman TN, Cushman SA, Wallin DO, Hayden J (2012) Multi scale habitat relationships of *Martes americana* in northern Idaho, U.S.A. USDA Forest Service RMRS Research Paper RMRS-RP-94

Wellenreuther M, Larson KW, Svensson EI (2012) Climatic niche divergence or conservatism? Environmental niches and range limits in ecologically similar damselflies. Ecology 93:1353–1366

Wereszczuk A, Zalewski A (2015) Spatial niche segregation of sympatric stone marten and pine marten—avoidance of competition or selection of optimal habitat? PLoS ONE 10:e0139852. doi:10.1371/journal.pone.0139852

Wiens J, Rotenberry JT, van Horne B (1987) Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132–147

Yackulic CB, Chandler R, Zipkin EF, Royle JA, Nichols JD, Campbell Grant EH, Veran S (2013) Presence-only modelling using MAXENT: when can we trust the inferences? Methods Ecol Evol 4:236–243

Zalewski A, Włodzimierz JW (2006) Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieza Forest (E Poland) compared with other European woodlands. Ecography 29:31–43

Zalewski A, Jedrzejewski W, Jedrzejewska B (2004) Mobility and home range use by pine martens (*Martes martes*) in a Polish primeval forest. Ecoscience 11:113–122