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Far from the madding crowd: Tolerance toward human disturbance shapes distribution and connectivity patterns of closely related *Martes* spp.

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Abstract

To assess niche overlap between the most similar European sympatric carnivores, the pine marten *Martes martes* and stone marten *Martes foina*, and outline their potential distributions and connectivity corridors in Central Italy, we applied a multivariate kernel density procedure which allowed to assess both species' ecological hypervolumes based on a set of 16 environmental predictors and used the resulting probability of occurrence map as a resistance surface in electrical circuit theory-based models. Distance to watercourses and percent cover of deciduous forest and shrubland were the most relevant factors shaping pine marten ecological niche, while stone marten distribution was mainly shaped by human population density and cover of both human settlements and deciduous forest. Overlap between the hypervolumes of the two martens was low-to-moderate, while, on average, landscape connectivity was higher for the stone marten. The inclusion in the models of human disturbance-related variables enabled to define a possible mechanism driving habitat partitioning in human-altered landscapes. Based on our results, increasing human density and urbanization of European lowland and hilly landscapes are expected to represent a greater threat to the pine marten than the stone marten.

KEYWORDS

diel activity, ecological niche models, Hutchinsonian hypervolume, marten, niche overlap

1 | INTRODUCTION

In the last decades, ecologists and biogeographers have spent great effort to develop accurate methods for estimating species' distribution in relation to biotic and abiotic conditions. Currently, species occurrences are widely used in combination with predictor variables for developing ecological niche models (ENMs; also known as species distribution models or habitat suitability models; Guisan et al., 2013). Assuming that species' locations reflect their ecological preferences, ENMs can be used to explore the correlation between presence data and environmental variables and assess range overlap and niche divergence in related species (Wellenreuther, Larson, & Svensson, 2012).

In the last 20 years, methods to develop ENMs have spread (Lobo, Jiménez-Valverde, & Hortal, 2010). However, positive or negative associations among species have been often ignored so far, notwithstanding ENMs would benefit from more realistic analyses involving inter-species relationships, especially for closely related species.

Actually, biological interactions (e.g., competition, predation, parasitism; Bascompte, 2009; Van Dam, 2009),

physical constrains (habitat connectivity; van Langevelde, van der Knaap, & Claassen, 1998; Baguette & Mennechez, 2004; van Langevelde, 2015) and historical factors (colonization history; Ovaskainen & Hanski, 2002; Remonti, Prigioni, Balestrieri, Sgrosso, & Priore, 2008) often constrain Hutchinson's *fundamental niche* (1957) into a *realized niche.* In the biogeographical context, accessible areas fulfilling a species' abiotic and biotic requisites constitute its distribution range or realized distribution (Peterson & Soberón, 2012; Soberón & Peterson, 2005).

Because closely related, morphologically similar species commonly share ecological requirements, interspecific relationships are a major biological factor that can restrict the potential distribution and abundance of the less competitive species (MacArthur, 1972). Accordingly, sympatric, closely related mammalian species often display microhabitat or macrohabitat segregation, supporting the need for interpreting ENMs in a multispecific context (Anderson, Peterson, & Gómez-Laverde, 2002).

As an example, invasive North American mink *Neovison vison* accelerated the decline of European mink *Mustela lutreola* (Maran & Henttonen, 1995; Põdra, Gómez, & Palazón, 2013) while, in turn, Eurasian otter *Lutra lutra* has been reported to reduce North American mink density (Bonesi & Macdonald, 2004). Fluctuations in the abundance of sympatric related species occur frequently and long-term coexistence may be the overall result of a history of reciprocal declines and recoveries (Powell & Zielinski, 1983).

The closely related pine marten *Martes martes* and stone marten *Martes foina* (Koepfli et al., 2008) are the most similar European sympatric carnivores (Larroque, Ruette, Vandel, & Devillard, 2015). They are comparable in size, morphology and feeding habits (Balestrieri et al., 2011; Balestrieri, Remonti, Capra, Canova, & Prigioni, 2013; Marchesi, 1989), with extensively overlapping trophic niches (Posluszny, Pilot, Goszczynski, & Gralak, 2007; Remonti et al., 2012). Both species coexist over a large area (Mitchell-Jones et al., 1999) and prefer forested habitats; nonetheless, when syntopic, the pine marten generally occupies forested areas, while the stone marten occurs in rural and suburban areas (Vergara, Cushman, Madeira, & Ruiz-González, 2017; Virgós, Zalewski, Rosalino, & Mergey, 2012). Stone marten association with fragmented and urbanized habitats has been explained as the result of competition with the pine marten (Delibes, 1983), although the mechanisms which should make the latter more competitive are still not clear (but see Torretta et al., 2017).

Although several studies have been conducted on morphological variation and character displacement in small- and medium-sized mustelids (e.g., Dayan & Simberloff, 1994; Loy, Spinosi, & Carlini, 2004; Meiri & Dayan, 2003), only a few recent studies have addressed the habitat preferences of both martens in syntopy (Larroque et al., 2015; Larroque, Ruette, Vandel, & Devillard, 2017; Vergara, Cushman, Madeira, & Ruiz-González, 2017; Vergara, Cushman, Urra, & Ruiz-González, 2015; Wereszczuk & Zalewski, 2015). By applying multiscale, habitat suitability models Vergara et al. (2015) compared pine marten and stone marten habitat use at the southern limit of pine marten distribution in Spain, recording a clear spatial segregation and niche divergence, with the pine marten often displacing the stone marten from forested landscapes (see also Vergara, Cushman, Madeira, & Ruiz-González, 2017; Vergara, Cushman, & Ruiz-González, 2017).

Nonetheless, none of the ENMs applied till now allows to quantify species niches by delineating the shape, volume and overlap of an entire hypervolume (Blonder, Lamanna, Violle, & Enquist, 2014), that is, the set of points within the *n*-dimensional space which reflects suitable values of the *n* variables (Hutchinson, 1957). Blonder et al. (2014) recently proposed a multivariate kernel density procedure intended to quantify high-dimensional ecological hypervolumes from a set of observations. Briefly, hypervolumes are computed across kernel density estimation (KDE), importance-sampling Monte Carlo integration and range-testing techniques, overcoming computational inefficiencies that limited previous methods to low-dimensional systems (for a detailed description see Blonder et al., 2014, Blonder, 2018). Multivariate KDE has been then applied in several fields of research, that is, to investigate the usefulness of forest inventories data (Brandl et al., 2014), global invasion patterns (*Rhinella marina*; Tingley, Vallinoto, Sequeira, & Kearney, 2014), processes causing the latitudinal gradient in species richness (Lamanna et al., 2014), nest-site niches (*Ammodramus* spp.; Kern, 2015), niche diversity (European freshwater species; Iversen, Jacobsen, & Sand-Jensen, 2016), genetic differentiation patterns (*Malayemys* spp.; Ihlow et al., 2016), biotic responses to climatic extreme events (Schweiger, Audorff, & Beierkuhnlein, 2015) and land use changes (Barros, Thuiller, Georges, Boulangeat, & Münkemüller, 2016; Milanesi, Breiner, Puopolo, & Holderegger, 2017).

We used *n*-dimensional hypervolumes to assess the current potential distributions and niche overlap of pine marten and stone marten at a regional-scale in central Italy. Although both species have been reported to be widely distributed in the Italian peninsula, recent studies have highlighted that their distribution is not uniform and they tend to segregate in space. As an example, the recent expansion of the pine marten in apparently unsuitable lowland areas of NW Italy (Balestrieri et al., 2016; Balestrieri et al., 2016) or in forested hills of central Italy (Mori, Menchetti, Dondini, Biosa, & Vergari, 2014) seems to have coincided with a contraction in the local stone marten range, whereas there are wide forested areas, both on the Alps (Mosini et al., 2017; Patriarca & Debernardi, 1997) and the Apennines (Vercillo & Ragni, 2010), where the latter is the dominant marten species. This pattern suggests that competition

may play a major role in shaping the distribution of *Martes* spp. and thus we may expect that each species will not necessarily be found in all habitats within a map pixel of predicted potential distribution.

Thus we compared pine marten and stone marten habitat selection in an area of sympatry with the aim of disentangling the roles played by environmental characteristics and interspecific competition in shaping the distribution of each species.

Interacting with movement ecology, spatial heterogeneity and land use also affects dispersal and, consequently, the genetic structure of populations (Cushman, Shirk, & Landguth, 2012; Larroque, Ruette, Vandel, & Devillard, 2016; Mergey et al., 2017). In the Mediterranean region, pine marten gene flow is facilitated by forests and scrubland, while crops and anthropogenic barriers pose much greater resistance than optimal habitats (Ruiz-González et al., 2014). In contrast, elevation and topographical roughness are the main drivers of stone marten genetic differentiation (Vergara, Cushman, & Ruiz-González, 2017).

Recently, attention has shifted from the identification of a single ecological corridor between species locations to independent node-based models; individual paths through the landscape are modeled as movements of charge through an electrical circuit, with greater redundancy in travel routes between nodes (patches) enhancing flow between them (McRae, 2006; McRae, Dickson, Keitt, & Shah, 2008; Tournant, Afonso, Roué, Giraudoux, & Foltête, 2013). To identify the ecological corridors of both marten species, we used the probability of occurrence map resulting from *n*-dimensional hypervolumes as a resistance surface in electrical circuit theory-based models.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area corresponds to Tuscany region, central Italy (Figure 1), with an area of ca. 23,000 km^2 and a population of ca. 3.8 million inhabitants (160 ind./km^2). The area is crossed from the north-west to the south-east by the Apennines (25%), with hills making up about two-thirds (66.5%) of the region's total area (mean altitude of the region = 279 m a.s.l.). Lowlands cover less than 2,000 km^2, on the lower stretches of major rivers and the Tyrrhenian coast. Land cover is mainly forests (43.4%) and cultivated fields (43%). Shrubland covers ca. 4% of the territory, while the largest human settlements (4.7%) occur on the Tyrrhenian coast and in the northern part of the region, at the foot of the Apennines. Road density is slightly higher than the average for the country (58.3 vs. 56.5 km/100 km^2; total length = 4,922 km) and the mean number (±SE) of vehicles/hour is 557 ± 15 (http://www.regione.toscana.it/-/dati-di-traffico-sulle-strade-regionali). The climate is temperate sub-Mediterranean, fairly mild in coastal areas, and harsher and rainy in the interior, with large fluctuations in temperature between winter (T_{min} = −2 and −25°C, respectively) and summer (T_{max} = 35 and 4°C, respectively).

2.2 | Species data and predictor variables

Available marten occurrences were collected by checking on (a) citizen-science platforms (iNaturalist and NaturaeSocialMapping), (b) social networks (Facebook and Twitter) and (c) websites and online forums (i.e., YouTube, Flickr). All videos and pictures were subjected to a blind identification procedure by three of us (A.R.-G., E.M. and A.B.) and discordant records were discarded. In the absence of images, records were considered as reliable whenever forwarded by zoologists. We also checked the collections of the regional museums of Firenze ("La Specola"), Grosseto ("Maremma") and Calci (University of Pisa) and reviewed available checklists (e.g., De Marinis & Lapini, 1994; Fazzi & Lucchesi, 2016; Mori et al., 2014). Finally, we included some records from the databases of two of us (E.M. and M.M.). We considered only the occurrences recorded since the beginning of the century (2000–2016).

Overall, we collected 139 unequivocal occurrences for the pine marten and 113 for the stone marten (Figure 1) of which 178 (70.6%; 97 stone and 81 pine martens) were road-kills, 48 (19.0%) camera-trapped individuals and 26 (10.3%) museum data. The chi-squared test (χ^2) was used to test for inter-specific variation in the source of records. All species locations were georeferenced in the UTM WGS84 32 N coordinate system using ArcGIS 10.1 (ESRI, Redlands, CA, www.esri.com/software/arcgis; S1 Table).

We considered 16 predictor variables for which continuous spatial data were available for the whole study area. Relevant environmental variables were selected based on previous studies (Balestrieri, Bogliani, et al., 2016; Vergara et al., 2015; Wereszczuk & Zalewski, 2015) and available knowledge on both martens' ecology (Virgós et al., 2012 and references therein).

Topographic variables such as altitude and slope were derived from a digital elevation model of Italy with a spatial resolution of 20 m (http://www.sinanet.isprambiente.it; Table 1), while bioclimatic variables (annual mean temperature, annual temperature range, annual precipitation and isothermality; the latter quantifies how large the day-to-night temperatures oscillate relative to the annual oscillations) were derived from the Worldclim data set (version 2.0; http://www.worldclim.org; Table 1). Percent covers of major forest types (deciduous vs. other woods), shrubland, cropland (including meadows) and human settlements were calculated from CORINE Land Cover 2012 (European Environment Agency; http://www.sinanet.isprambiente.it). From the same data source, we measured also the distance to either watercourses or human settlements, habitat diversity

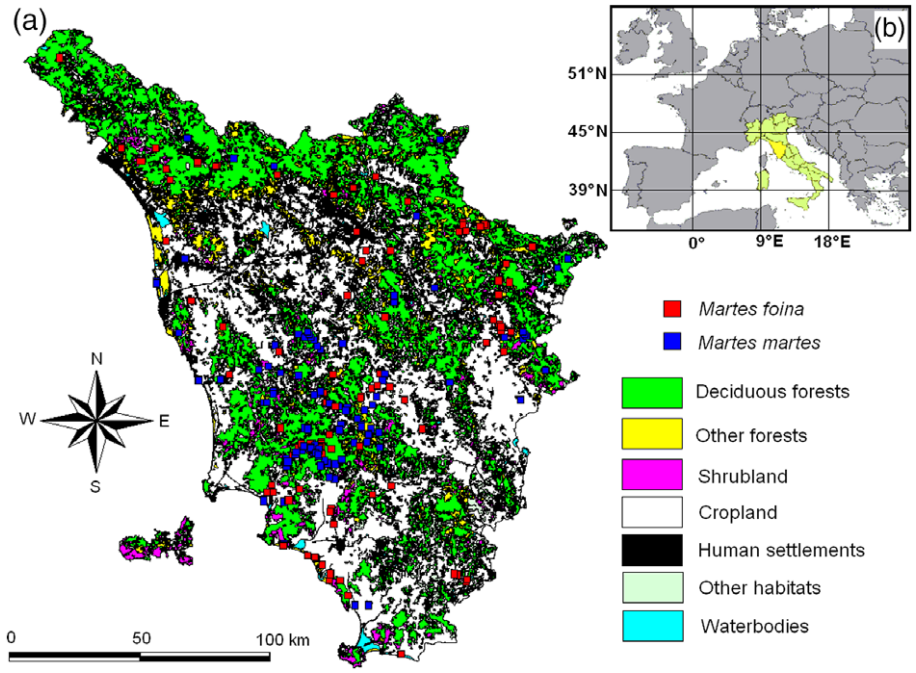

FIGURE 1 (a) Distribution of pine- and stone marten records in the study area, Tuscany region; (b) map of Europe showing the position of the study area (yellow) in Italy (green). Main habitats from CORINE land cover 2012 are also shown

TABLE 1 Variables used in the development of ecological niche models (CLC: corine land cover classes)

Variable	CLC	Unit	VIF	Pine marten	Stone marten
Altitude	-	m a.s.l.	2.7	4.79 (± 0.21)	5.56 (± 0.02)
Slope	-		2.4	5.47 (± 0.26)	6.52 (± 0.03)
Annual mean temperature	-	°C	> 3		
Isothermality	-	%	> 3		
Temperature annual range	-	°C·10	1.7	5.64 (± 0.24)	6.61 (± 0.03)
Annual precipitation	-	Mm	1.7	4.87 (± 0.21)	6.22 (± 0.03)
Deciduous forests	311, 523	%	2.1	7.61 (± 0.34)	9.74 (± 0.03)
Other forests	312, 313	%	1.3	7.59 (± 0.23)	8.61 (± 0.03)
Shrubland	322–24	%	1.2	7.95 (± 0.34)	5.64 (± 0.03)
Cropland	211–13, 221–24, 241–44, 422	%	> 3		
Shannon's index	-		1.3	7.21 (± 0.35)	6.16 (± 0.03)
Distance to watercourses	-	m	1.2	7.88 (± 0.35)	6.82 (± 0.03)
Distance to human settlements	-	m	1.5	7.46 (± 0.36)	5.41 (± 0.03)
Road density	-	Km/km^2	> 3		
Human settlements	111–12, 121–24, 131–33, 141–42, 334	%	2.0	6.54 (± 0.25)	10.14 (± 0.05)
Human population density		n/km^2	1.9	5.76 (± 0.24)	11.58 (± 0.05)

Note. Variables with a variance inflation factor (VIF) > 3 were removed from further analysis to avoid multi-collinearity. Percent variable importance (± *SD*) estimated through the *n*-dimensional hypervolume for the pine and stone marten is also shown.

(Shannon's Index) and road density. Moreover, we considered human population density (GEOSTAT 2011 grid dataset - Eurostat - European Commission; ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography) and road density (OpenStreetMap; www.openstreetmap.org) at a spatial resolution of 1 km. All predictor variables were resampled at a 1 × 1 km grid cell size.

To avoid multicollinearity among predictors, we calculated the variance inflation factor (VIF; Zuur, Ieno, & Elphick, 2010) for all variables using a stepwise method, that is, removing step by step the predictor with the highest VIF value (annual mean temperature, isothermality, percent cover of croplands and road density), until all predictors had values lower than the threshold (VIF < 3; Zuur et al., 2010). Spatial autocorrelation among each species' locations was

tested by Moran's I correlogram (Dormann et al., 2007): values ranged between −0.001 and 0.127, indicating no spatial autocorrelation among species locations.

2.3 | ENMs and niche overlap

First, we quantified Hutchinson's ecological niche for each species by developing *n*-dimensional hypervolumes (Blonder et al., 2014). This method allows the estimation of the ecological hyper-space based on the whole set of predictors by a multidimensional KDE procedure. Following Blonder et al. (2014), we initially transformed each predictor variable relative to its mean and *SD* and used bandwidth vectors (*h,* i.e., the parameters controlling the degree of smoothing applied to the data) estimated from the data by Silverman's estimator (Blonder et al., 2014). We chose a quantile threshold parameter (τ; the fraction of the probability density to be excluded from the hypervolume) of 0.05 and thus, for each species, included a random set of 95% of occurrences in the analyses. We used the inclusion test (Blonder et al., 2014) to quantify both species' distribution in our study area. Then, we calculated and compared the importance of predictor variables for both species and estimated the overlap between the hypervolumes of the two species (or "ecological niche overlap", i.e., shared volume / summed volumes; Blonder et al., 2014). We replicated this procedure 1,000 times in order to infer the spatial distribution of pine- and stone marten, assess their correlation through Spearman's coefficient (ranging between −1 and 1; 0 indicates no correlation) and provide an average (±*SD*) estimate of each predictor variable importance and niche overlap. All these analyses were performed using the HYPERVOLUME package v. 2.0.8 (Blonder et al., 2014) in the open-source software R (v. 3.1.2; https://www.r-project.org/).

Finally, we used Mann–Whitney's test to compare the mean values of environmental predictors as measured at a 1 × 1 km grid cell size for pine and stone marten recordsites.

2.4 | Landscape connectivity

Following previous studies (Della Rocca, Bogliani, & Milanesi, 2017; Milanesi et al., 2016; Milanesi, Holderegger, Caniglia, Fabbri, & Randi, 2016; Pullinger & Johnson, 2010; Spear, Balkenhol, Fortin, Mcrae, & Scribner, 2010; Wang, Yang, Bridgman, & Lin, 2008), we derived a resistance map for each species, defined as the inverse of the distribution map (1 – probability of occurrence) and combined it with circuit theory to explore landscape connectivity. Circuit theory models movement ecology via random walks across all available pathways, assuming that the intensity of flow between nodes (locations) is proportional to the number of times an individual goes from one node to another moving through the particular cell under consideration (McRae et al., 2008). In other words, the estimated flow corresponds to the probability of movement between nodes and thus identifies landscape connectivity patterns (McRae et al., 2008). Analyses were carried out by Circuitscape v.4.0.5 (McRae et al., 2008).

Specifically, Circuitscape considers simultaneously all possible pathways connecting nodes on a resistance-to-movement map, to produce a map of current density (equivalent to the probability of use by random walkers; Koen, Bowman, Sadowski, & Walpole, 2014). Following Pitman et al. (2016), to model connectivity independent from source and destination points (see also Koen et al., 2014) we developed a landscape permeability map by placing regularly distanced, random nodes in a 50 km buffer (>20% of the study area width; Koen et al., 2014) around the perimeter of the study area (except for the portion limited by the Tyrrhenian Sea). To identify the optimum number of random nodes required to generate an unbiased landscape connectivity map, up to 500 random nodes were placed at intervals of 10 and then Circuitscape was run to generate 50 permeability maps (Koen et al., 2014). After each iteration, we estimated Pearson' correlation coefficient between the resulting current density and those estimated from 10,000 random locations inside the study area (Koen et al., 2014; Pitman et al., 2016). A current density map was considered independent of node placement when the curve comparing correlation coefficients to the number of node pairs reached an asymptote (i.e., a slope of zero; Koen et al., 2014; Pitman et al., 2016). Following Della Rocca et al. (2017), the final current map (i.e., that with the optimal number of random nodes) was rescaled between 0 and 1 (indicating low and high landscape connectivity, respectively). The correlation between the final current maps of the two marten species was assessed by Spearman's correlation coefficient.

3 | RESULTS

Marten records were distributed throughout the study area, including coastal, hilly and mountainous areas up to 1,168 m a.s.l. (mean ± *SD* = 397 ± 188 and 367 ± 252 for *M. martes* and *M. foina*, respectively). Stone martens were recorded as roadkills more frequently than pine martens (85.8 vs. 58.3%; $\chi^2 = 22.8$, $p < 0.001$). Both species were mostly recorded into or close to wooded areas, which cover the central, hilly part of the region and the Apennines in the north (Figure 1).

The two 12-dimensional hypervolumes, representing estimates of the ecological niches of the pine- and stone marten, allowed to assess both the patterns of distribution of the two species in the study area (Figure 2) and relative importance of predictor variables (Table 1). Pine marten's hypervolume was smaller (61.7 d^{12}) than stone marten's (140.6 d^{12}); shrubland (7.95%), distance to watercourses (7.88%) and percent cover of forests (deciduous forests: 7.61%; other

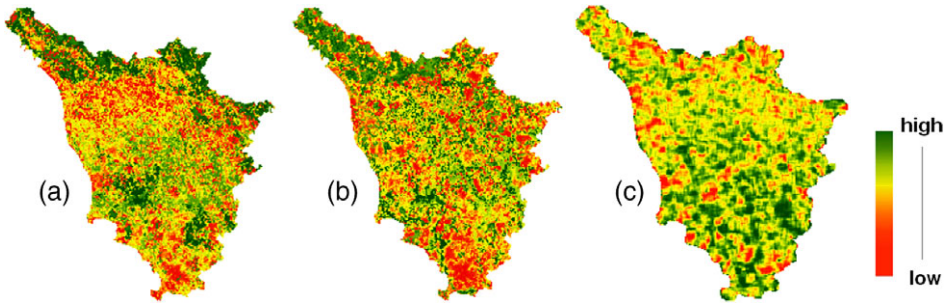

FIGURE 2 Average distribution of pine marten *Martes martes* (a) and stone marten *Martes foina* (b) estimated through 1,000 *n*-dimensional hypervolumes (red-green scale indicates lower-higher [0–1] probability of occurrence), and correlation (c) between pine- and stone marten distribution (Spearman's coefficient) in the study area (red-green scale indicates lower-higher [−1–1] correlation)

forests: 7.59%) were the most relevant factors shaping pine marten ecological niche, while stone marten distribution was mainly shaped by human population density (11.58%) and percent cover of both human settlements (10.14%) and deciduous forest (9.74%; Table 1).

Overlap between the hypervolumes of the two martens was 32.31 ± 11.79%, corresponding to an average spatial correlation of 30.49 (± 30.63) between their distributions (Figure 2). Moderate-to-high (>0.5) connectivity was assessed for 44.2% of pixels of stone marten's current map, while the percentage significantly decreased to 33.7% for the pine marten (chi-squared test: $\chi^2 = 535.05$, 1 d.f, $p < 0.001$). Landscape connectivity was higher for the stone marten (mean current densities ± *SD* at, respectively, 113 and 139 locations were 0.45 ± 0.19 and 0.39 ± 0.18), with an average spatial correlation of 0.32 ± 0.35 (Figure 3). Connectivity for the pine marten was the lowest on coastal and mostly urbanized or cultivated areas, while stone marten's movements were hindered by both large cultivated areas (southern part of the region) and large forested areas (north-western tip). Compared to stone marten, pine marten tended to avoid humans (mean human density: 157.7 vs. 464.1 ind./km^2, $U = 5{,}921.5$; mean percent cover of human settlements: 2.8 vs. 9.4, $U = 6{,}264.5$; distance to human settlements: 3.3 vs. 2.0 km, $U = 4{,}665.5$; $p < 0.01$ for all comparisons) and selected deciduous forests (percent cover: 45.9 vs. 33.6, $U = 5{,}831$, $p = 0.0013$), while stone marten occurred nearer to watercourses (distance to watercourses: 9.4 vs. 11.8 km, $U = 5{,}741$, $p = 0.0008$; Table 2, Figure 4).

4 | DISCUSSION

We applied the most recent and robust ecological niche and landscape connectivity modeling techniques to estimate ecological niche overlap between pine marten and stone marten and identify the most important predictors of their distribution in central Italy. The two species clearly differed in their tolerance toward human disturbance, as demonstrated by their different responses to the variables "percent cover of-" and "distance to human settlements" and "human population density", with the stone marten being by far more tolerant. This ecological flexibility may allow the stone marten to manage better than the pine marten in rural and even urban areas wherever residual woods still offer some shelter (Genovesi, Sinibaldi, & Boitani, 1997; Sacchi & Meriggi, 1995; Virgós et al., 2012). In this context, the lower "distance to water" recorded for the stone marten may indicate its selection for residual riparian woods, which often represent the only vegetation cover in agricultural landscapes (Balestrieri et al., 2015; Rondinini & Boitani, 2002). Variation in each species' tolerance for human disturbance was consistent with patterns of resting sites, a key resource for both species (Gough & Rushton, 2000), with the stone

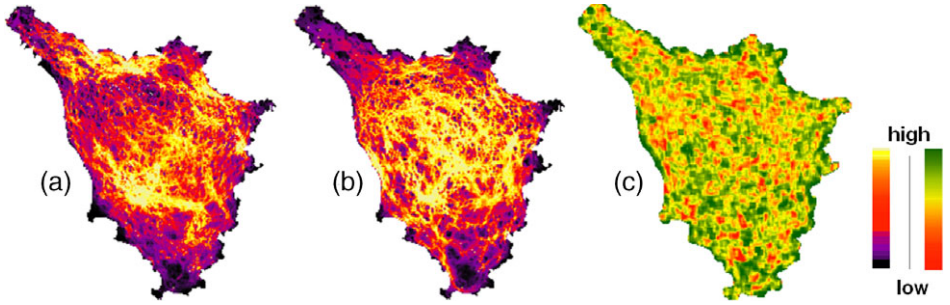

FIGURE 3 Current map for pine marten *Martes martes* (a) and stone marten *Martes foina* (b) derived from resistance surface using Circuitscape software (black-yellow scale indicates lower-higher [0–1] connectivity), and correlation (c) between pine- and stone marten current maps (Spearman's coefficient) in the study area (red-green scale indicates lower-higher [−1–1] correlation). Current densities through cells indicate the probability of a random walker passing each cell as it moves from one patch to the other

TABLE 2 Values of environmental predictors as measured at a 1 × 1 km grid cell size for pine- and stone marten record-sites

	Martes martes			*Martes foina*		
Variable	**Mean**	***SD***	**Min–max**	**Mean**	***SD***	**Min–max**
Altitude	406.0	180.8	3.7–884.7	370.6	250.8	2.1–1,168.5
Slope	2.9	2.0	0.02–9.7	3.1	2.9	0.01–14.9
Temperature annual range	254.5	9.7	237–289	257.1	13.4	230–287
Annual precipitation	742.0	63.2	588–929	766.1	95.8	588–950
Deciduous forests	45.9	33.9	0.0–100	33.6	34.7	0.0–100
Other forests	5.6	16.1	0.0–87.5	6.3	17.2	0.0–100
Shrubland	7.9	14.1	0.0–93.7	5.6	11.8	0.0–56.2
Shannon's index	1.2	0.3	0.7–1.7	1.2	0.3	0.71–1.8
Distance to watercourses	11,784	5,375	2,236–28,792	9,418	5,466	0.0–21,260
Distance to settlements	3,226	1,999	0.0–9,681	1,975	1,744	0.0–7,967
Human settlements	2.9	11.6	0.0–100	9.4	21.4	0.0–100
Human population density	157.7	434.4	0.0–3,682	464.1	1,027.5	0.0–4,275

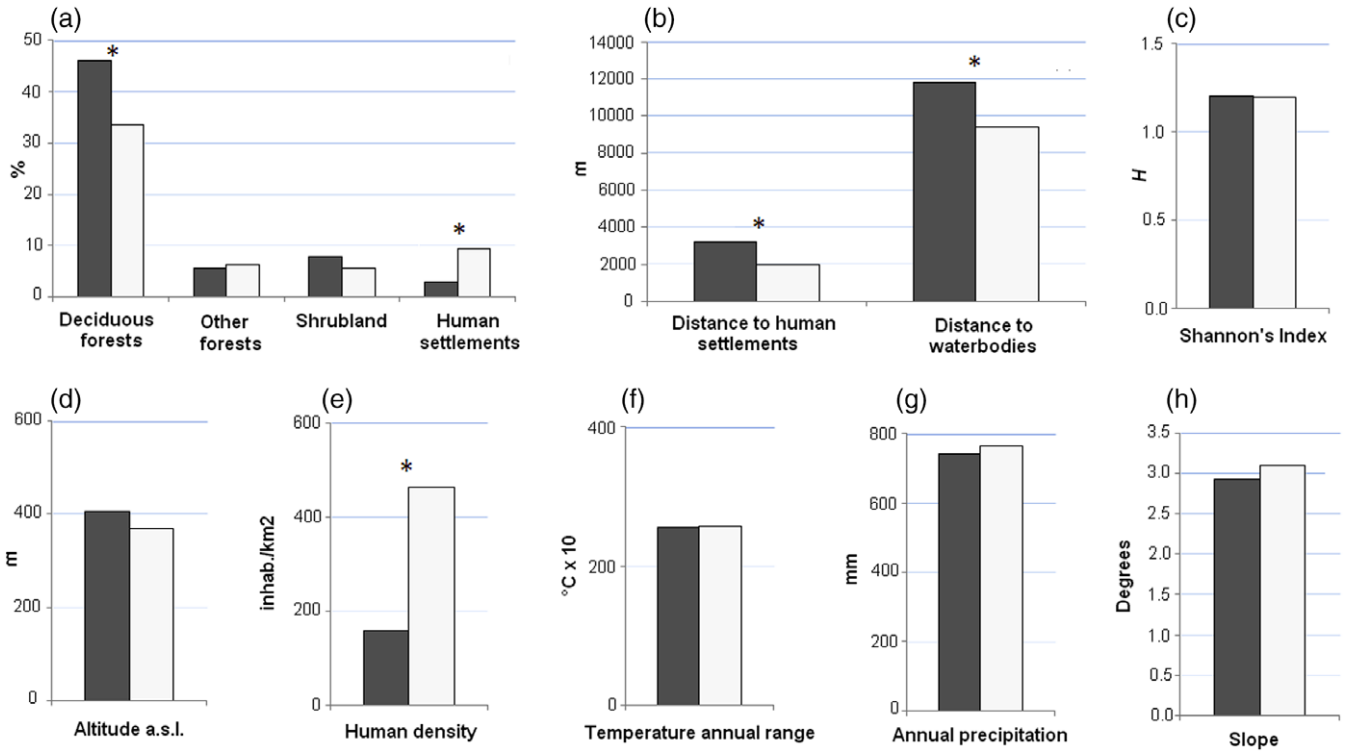

FIGURE 4 Mean values of 12 environmental variables [(a) Percent cover of major habitat types; (b) Distance to either human settlements or waterbodies; (c) Shannon's index; (d) Altitude above sea level; (e) Human density; (f) Temperature annual range; (g) Annual precipitation; (h) Slope], as measured at a 1 × 1 km grid cell size for pine marten *Martes martes* (dark bars) and stone marten *Martes foina* (light-gray bars) record-sites. Asterisks indicate significant differences (Mann–Whitney's test, $p < 0.0025$ for all comparisons)

marten establishing its resting sites both in open and forest habitats while those of the pine marten occur almost exclusively in forests (Larroque et al., 2015).

Unexpectedly, "shrubland" was the most important variable of pine marten's hypervolume. The suitability of this habitat for the pine marten has been pointed out by previous studies on Mediterranean islands (Elba: De Marinis & Masseti, 1993; Minorca: Clevenger, 1994; Sardinia: Lombardini et al., 2015), where this species does not seem to show any clear preference for forested habitats. Recently, selection for shrub by radiotracked individuals has been reported also for eastern France (Larroque et al., 2017). Pine marten occurrence in high and dense shrubland has been associated to both cover and availability of its main prey, namely small rodents (Caryl, Quine, & Park, 2012; Clevenger, 1994). Moreover, in fragmented habitats shrubland may play a major role in forest connectivity (Ruiz-González et al., 2014). In our study area small shrub patches (on average 1.13 km^2) are mainly located close to- or dispersed throughout forests, also as a consequence of recent coppicing activities, and thus may both act as connectors between forest patches and represent suitable hunting grounds for pine

martens. Accordingly, small rodent density has been recently reported to be higher in recent coppices providing high shrub-cover than in high forest stands (Gasperini et al., 2016).

Forest cover affected the occurrence of both martens. On average, deciduous forests cover was the highest for pine marten's occurrences, consistently with pine marten's ability of outcompeting the stone marten in these habitats (Balestrieri, Ruiz-González, et al., 2016; Delibes, 1983).

Consequent to their differential use of forests and human settlements, ecological niche overlap between the two species was low-to-moderate, lowering interspecific competition and allowing their coexistence in the highly heterogeneous landscape of the hilly study area, where wood- and shrub patches are still interspersed with cultivated field and urban areas.

Although both the role of forested habitat as key features for martens and the avoidance of urban and open areas by the pine marten are well-known behavioral patterns of these mustelids (review by Virgós et al., 2012; Vergara et al., 2015; Zub, Kozieł, Siłuch, Bednarczyk, & Zalewski, 2018), our analyses allowed to point out the effect of each species' tolerance toward human disturbance in shaping their relative patterns of distribution. What may be the origin of such different behavioral attitudes in these two prototypically similar (Larroque et al., 2015) species? While the pine marten was described as mainly nocturnal with bouts of daily activity (Clevenger, 1992) or facultative nocturnal (Monterroso, Alves, & Ferreras, 2014), recently Torretta et al. (2017) and Fonda, Torretta, Balestrieri, and Pavanello (2017) showed through camera-trapping in Northern Italy that it may be better defined as cathemeral, with up to 60% of diurnal recordings. In Tuscany, available radiotracking data indicate that the pine marten is active throughout the diurnal cycle (Del Fante, 2012). In contrast, the stone marten is strictly- (Monterroso et al., 2014; Torretta et al., 2017) or mainly- (Llorente-Rodríguez, Nores-Quesada, López-Sáez, & Morales-Muniz, 2015; Posillico, Serafini, & Lovari, 1995) nocturnal. While cathemerality may enhance pine marten fitness by lowering intraguild competition in forested habitats (Torretta et al., 2017), in densely human-populated areas, day-light activity is likely to be detrimental, increasing the probability of conflicts with humans, road-mortality and illegal hunting (Bateman & Fleming, 2012). Accordingly, while habitat fragmentation and expanding wildland-urban interface (sensu Radeloff et al., 2005) are considered a serious threat to pine marten throughout its distribution range (Proulx et al., 2004; Ruiz-González et al., 2014; Ruiz-González, Cushman, Madeira, Randi, & Gómez-Moliner, 2015), stone marten´s geographic range is expanding due to its lower vulnerability to anthropogenic impacts (Abramov, Kranz, Herrero, Choudhury, & Maran, 2016; Herr, Schley, & Roper, 2009; Proulx et al., 2004).

Genetic studies on several pine marten populations have pointed out that anthropogenic land cover types hinder gene flow because of their high resistance to pine marten movements (Larroque et al., 2016; Mergey et al., 2017; Ruiz-González et al., 2014, 2015). Consistently, landscape connectivity was lower for the pine marten, particularly in the north-western sector of the region including the largest conurbations, and on the Tyrrhenian coast, where human density is the highest. Anyway, a large low-connectivity area for both marten species coincided with the most agricultural province (Grosseto), in the southern part of Tuscany, in agreement with both martens' tendency to avoid large open habitats. Moreover, large forested areas, as those occurring on the Apennines, seem to act as a barrier to stone marten's movements. Resistance may depend on either interspecific/intraguild competition or the actual stone marten preference for more open habitats. While widespread occurrence of stone martens in forested areas where the pine marten is absent (Mosini et al., 2017) would support the latter hypothesis, our data do not allow to rule out the role of competition.

Although ENMs have the benefit of avoiding subjective expert opinions (Milanesi, Holderegger, Caniglia, Fabbri, Galaverni, & Randi, 2016; Milanesi, Holderegger, Caniglia, Fabbri, & Randi, 2016; Wang et al., 2008), which can potentially bias resistance surfaces due to insufficient knowledge about both the ecology of the target species and real distribution of corridors and barriers to its movements in the area of interest (Della Rocca et al., 2017; Stevenson-Holt, Watts, Bellamy, Nevin, & Ramsey, 2014; Zeller, McGarigal, & Whiteley, 2012), our Geographic Information System (GIS)-based models inevitably have some limitations and their accuracy should be tested by field data. Particularly, the role played by shrubland and anthropogenic barriers needs to be validated by fine-scale, radiotracking or fecal DNA-based studies. As an example, using path selection functions to analyze radiotracking data, Carvalho, Carvalho, Mira, and Beja (2016) showed that, for genets (*Genetta genetta*), connectivity is influenced by the distribution of human infrastructures, while non-invasive genetic methods allowed to point out that pine marten expansion in NW Italy has been driven by riparian corridors (Balestrieri, Ruiz-González, et al., 2016).

5 | CONCLUSIONS

By combining Hutchinson's ecological niche and landscape connectivity, we assessed niche overlap between strictly related pine marten and stone marten and highlighted the role played by environmental factors in shaping their relative distribution in sympatry. With respect to previous studies (Vergara et al., 2015; Vergara, Cushman, Madeira, & Ruiz-González, 2017; Wereszczuk & Zalewski, 2015; Zub et al., 2018), the inclusion in the models of human disturbance-

related variables enabled for the first time to define a possible mechanism, depending on circadian activity patterns, driving habitat partitioning in anthropogenically altered landscapes (and, potentially, also explaining pine marten dominance in forested habitats; Torretta et al., 2017). Interestingly, a similar pattern has been proposed to explain the distribution of archeological records of both martens in the second half of the Holocene (Llorente-Rodríguez et al., 2015). As both ecological niche and connectivity are major criteria for site selection by conservationists (Tuomisto, 2010), *n*-dimensional hypervolumes and circuit theory could be an effective tool for landscape management, allowing to predict where landscape modifications are likely to alter environmental suitability for a target species. In the case of *Martes* spp., the pine marten appears to be less capable than the stone marten to adapt to the increasing human density and urbanization of European lowland and hilly landscapes. On the other hand, the progressive abandonment of farmland and consequent reforestation are expected to favor pine marten expansion to the detriment of the stone marten in low-productivity areas (Mosini et al., 2017).

Currently, road casualties are the main direct human cause of mortality for many mammals (Forman & Alexander, 1998), including martens (Haigh, 2012; Vercayie & Herremans, 2015). In our study area, the stone marten paid to road traffic the heaviest toll, but traffic may become a major cause of mortality also for pine marten expanding in lowlands of north-western Italy (Balestrieri, Bogliani, et al., 2016). Ecological corridors can enhance connectivity in deeply human-altered habitats (Balestrieri et al., 2015; Carvalho et al., 2016) and their role should be kept in mind when planning new infrastructures. In the next future wildlife corridors are expected to play an increasingly critical role in the conservation of forest-dwelling species (Carvalho et al., 2016; Clevenger, Wierzchowski, Chruszcz, & Gunson, 2002) and mitigation measures should be addressed to maintain or restore ecological flows in urban and agricultural landscape matrices.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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