Patchiness of forest landscape can predict species distribution better than abundance: the case of a forest-dwelling passerine, the short-toed treecreeper, in central Italy

Marco Basile[1,2,3], Francesco Valerio[4], Rosario Balestrieri[1,2], Mario Posillico[1,5], Rodolfo Bucci[5], Tiziana Altea[5], Bruno De Cinti[1] and Giorgio Matteucci[6]

[1] Istituto di Biologia Agroambientale e Forestale, Consiglio Nazionale delle Ricerche, Monterotondo Scalo, Italy
[2] Coordinamento MItO2000, Parma, Italy
[3] Chair of Wildlife Ecology and Management, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany
[4] CIBIO/InBIO-UE—Research Center in Biodiversity and Genetic Resources, Pole of Évora Applied Population and Community Ecology Laboratory, University of Évora UBC—Conservation Biology Lab, Department of Biology, Évora, Portugal
[5] Ufficio Territoriale Biodiversità di Castel di Sangro-Centro Ricerche Ambienti Montani, Corpo Forestale dello Stato, Castel di Sangro, Italy
[6] Istituto per i Sistemi Agricoli e Forestali del Mediterraneo, Consiglio Nazionale delle Ricerche, Ercolano (Na), Italy

ABSTRACT

Environmental heterogeneity affects not only the distribution of a species but also its local abundance. High heterogeneity due to habitat alteration and fragmentation can influence the realized niche of a species, lowering habitat suitability as well as reducing local abundance. We investigate whether a relationship exists between habitat suitability and abundance and whether both are affected by fragmentation. Our aim was to assess the predictive power of such a relationship to derive advice for environmental management. As a model species we used a forest specialist, the short-toed treecreeper (Family: Certhiidae; *Certhia brachydactyla* Brehm, 1820), and sampled it in central Italy. Species distribution was modelled as a function of forest structure, productivity and fragmentation, while abundance was directly estimated in two central Italian forest stands. Different algorithms were implemented to model species distribution, employing 170 occurrence points provided mostly by the MITO2000 database: an artificial neural network, classification tree analysis, flexible discriminant analysis, generalized boosting models, generalized linear models, multivariate additive regression splines, maximum entropy and random forests. Abundance was estimated also considering detectability, through N-mixture models. Differences between forest stands in both abundance and habitat suitability were assessed as well as the existence of a relationship. Simpler algorithms resulted in higher goodness of fit than complex ones. Fragmentation was highly influential in determining potential distribution. Local abundance and habitat suitability differed significantly between the two forest stands, which were also significantly different in the degree of fragmentation. Regression showed that suitability has a weak significant effect in explaining increasing value of abundance. In particular, local abundances varied both at low and high suitability

values. The study lends support to the concept that the degree of fragmentation can contribute to alter not only the suitability of an area for a species, but also its abundance. Even if the relationship between suitability and abundance can be used as an early warning of habitat deterioration, its weak predictive power needs further research. However, we define relationships between a species and some landscape features (i.e., fragmentation, extensive rejuvenation of forests and tree plantations) which could be easily controlled by appropriate forest management planning to enhance environmental suitability, at least in an area possessing high conservation and biodiversity values.

INTRODUCTION

In recent years, considerable research effort has been involved in studying the influence of landscape patterns on biodiversity, triggered by the wide availability of biological data, as well as by the development of sophisticated species distribution models (SDMs), capable of predicting the presence of a species as a function of environmental variables (*Elith & Leathwick, 2009*). The reliability of SDMs is based on the quality of occurrence data and the use of environmental predictors linked to species occurrence (*Austin, 2007*). For instance, presence data collected through nationwide standardised monitoring programmes provide enormous advantages in using SDMs, due to the creation of large databases (*Elith & Leathwick, 2009*), hosting large amounts of occurrences and covering a wide, biologically significant area. Appropriate environmental predictors are those supposed to best describe the set of abiotic and biotic conditions affecting species occurrence, i.e., those characterising the species ecological niche (*sensu* Hutchinson; *Hutchinson, 1957*; *Holt, 2009*). Indeed, large-scale species distribution modelling can be useful for addressing species-habitat relationships at multiple spatial scales in order to understand the spatial variability in habitat selection (*Farashi, Kaboli & Karami, 2013*; *Chefaoui et al., 2015*; *Morand et al., 2015*). Also, considering the spatial heterogeneity in the environment has become essential in many studies regarding reproduction, meta-population dynamics, gene flow, dispersal and connectivity (*Bender, Tischendorf & Fahrig, 2003*; *Wang et al., 2008*; *Ryberg et al., 2013*). Recent studies have addressed this issue to propose alternative conservation strategies (*Nixon et al., 2014*), to monitor landscape change (*Darvishi, Fakheran & Soffianian, 2015*) and to give insight into the distribution of native and non-native species (*Kumar, Stohlgren & Chong, 2006*). Moreover, spatial patterns are considered major drivers of many ecosystem processes (*Uuemaa, Mander & Marja, 2013*).

Although landscape heterogeneity may promote biodiversity due to the increase in habitat types (i.e., spatial heterogeneity) (*Wiens, 1976*; *Loehle et al., 2005*; *Schindler et al., 2013*), a highly diverse landscape arising from anthropogenic fragmentation may result in the loss of natural habitats and specialist species, which frequently require large patches of relatively unaltered habitat (e.g., extensive areas of well-preserved forests) (*Marvier, Kareiva & Neubert, 2004*). Therefore, fragmentation can sometimes produce a simplification of

the biological community, or biotic homogenisation across the landscape (*McKinney & Lockwood, 1999*). Such a consequence derives from the loss of unique habitats, which are not replaceable in the short term (*Fahrig, 2003*).

Species abundance is also influenced by spatial variability, being affected by spatial gradients in the environmental parameters that form the environmental niche (*Martínez-Meyer et al., 2013*). Optimal conditions can be found where the environmental parameters are close to the centroid of the Hutchinsonian niche (*Hutchinson, 1957*). Hence, environmental variability can influence both the presence and abundance of a species. Indeed, the decrease in abundance could warn about a species decline in population and/or range extent earlier than a decrease in environmental suitability. In fact, abundance could also be low in highly suitable regions, in response to local limiting factors (*VanDerWal et al., 2009*).

The aim of our study was to investigate the relationship between environmental suitability and abundance of a species, in response to fragmentation. However, true environmental suitability can be expressed only by the whole set of environmental predictors and the local conditions that can influence movements and interaction (*Grinnell, 1917*) and the persistence of those conditions itself (*Jackson & Overpeck, 2000*). Such an approach may be unfeasible, as in our case. Therefore, we refer to a restricted set of factors influencing local or regional environmental suitability, i.e., some environmental predictors, which are supposed to be related to the probability of occurrence, and concern habitat suitability (HS) (*Franklin, 2009*). Among those habitats that can be highly modified by human activities, our research focused on forests, where unsustainable timber harvest can result in a patchy landscape and alter the habitat, adversely affecting forest biodiversity (*Donald et al., 1998*; *Penman, Mahony & Lemckert, 2005*; *Craig, 2007*; *Bearer et al., 2008*; *Shifley et al., 2008*; *Czeszczewik et al., 2014*; *Calladine et al., 2015*; *Escobar et al., 2015*). Woody plants are key elements in shaping the distribution of several bird species *such as* birds (*MacArthur, Recher & Cody, 1966*; *Cody, 1985*). Landscape structures and the spatial arrangement of habitat patches can affect both the abundance and distribution of birds, acting as structural bio-modifiers (*Uuemaa, Mander & Marja, 2013*).

Therefore, we selected as a model species a forest specialist bird, the short-toed treecreeper (Family: Certhiidae; *Certhia brachydactyla* Brehm, 1820), and used landscape metrics as well as forest variables to characterise the forest landscape and weight habitat suitability. The short-toed treecreeper is considered a forest-dwelling passerine, and hence a forest specialist, being a secondary cavity nester (*Newton, 1994*). It is usually found in oak or mixed-deciduous forests (with prevalence of oak), where it nests inside small holes excavated by woodpeckers or left by dead branches (*Cramp, 1988*). It is a resident species, with very limited movements, usually restricted to post-juvenile dispersal (*Cramp, 1988*). Home range and territory size can also be very limited, sometimes less than 1 ha (*Cramp, 1988*). The global range extends through most of central/southern Europe, up to Turkey and the Caucasus, overlapping with *C. familiaris* in central Europe (*BirdLife International, 2016*). Thus, we assessed whether there was a relationship between local abundance and HS. We hypothesise that the realized niche can be altered by fragmentation, resulting in lower HS and abundance. If such a relationship emerges, we aim to estimate its predictive power and usefulness in forest management and in conservation policies. In addition, we

modelled HS with several algorithms and compared results, to assess whether different species distribution models (SDMs) follow the same pattern of response.

METHODS

One of the main advantages offered by SDMs relies on the use of occurrence data collected with different methods (*Tsoar et al., 2007*). Therefore we used occurrence records from multiple sources, that spanned from year 2000 to 2013. We relied mainly on the MITO2000 database (*Monitoraggio Italiano Ornitologico*, Italian Ornithological Monitoring), an ongoing project which started in 2000 and operates at a country-wide level (*Fornasari et al., 2010*). The project uses point counts with unlimited radius (*Blondel, Ferry & Frochot, 1981*), sampling points being randomly selected within a 1 km² grid square in the region of interest. Point counts were carried out during a short time frame, from mid-May to mid-June. Occurrences of *C. brachydactyla* were also extracted from the databases of the National Forest Service (Ufficio Territoriale della Biodiversità, Castel di Sangro, AQ), and the LIFE+ ManFor C.BD project, which employed a sampling design similar to MITO2000, albeit at a smaller spatial scale (∼200–500 m). The spatial coverage of the occurrences was limited to the administrative boundaries of the regions of Lazio, Abruzzo and Molise, comprising 32,523 km², of which over one-third (12,309 km²) had forest cover (Fig. 1). The whole database was filtered from all the pseudo-replicated points that fell into the same 1 km² grid. The database was further cleared of all the occurrences that were located in unrealistic locations (i.e., non-forested areas), except for those <300 m away from the nearest forest patch, which were relocated to the nearest patch. Every occurrence was georeferenced with GPS. Hence, for our purposes, the error in location was assumed to be the same across the three datasets. The final database consisted of 170 occurrence points of *C. brachydactyla* (Table 1), of which 119 were supplied by the MITO2000 database, exceeding the recommended minimum sample size (*Wisz et al., 2008*).

Species distribution models

The SDMs were implemented using five environmental predictors, correlated with forest structure, productivity and the degree of fragmentation, at a spatial resolution of 30 m. First, a habitat type map, consisting of 12 classes, was created from the regional forest maps (*Marchetti, Chiavetta & Santopuoli, 2009*; *Garfí & Marchetti, 2011*; *Open Data Lazio, 2012*), aggregating all of the non-forest habitat and distinguishing 11 forest types (Table 1). Three landscape metrics were then calculated from the habitat map, using FRAGSTATS v. 4 software (*McGarigal, Cushman & Ene, 2012*): (1) *Diversity* (H'), a measure of patch type diversity within the landscape (*Shannon & Wiener, 1949*); (2) *edge density* (ED) which expresses the density (m ha^{-1}) of boundaries; (3) the *aggregation index* (AI) which measures the degree of aggregation between forest patches (*He, Dezonia & Mladenoff, 2000*). The first two metrics were implemented using a moving window of 1,000 m, as they can show little variability among different spatial scales and we were interested in landscape features, avoiding the influence of small patches (*Uuemaa, Roosaare & Mander, 2005*). By contrast, for AI a 300 m moving window was used, as we were interested, in this case, in controlling how small patches aggregate across the landscape, according also to the home
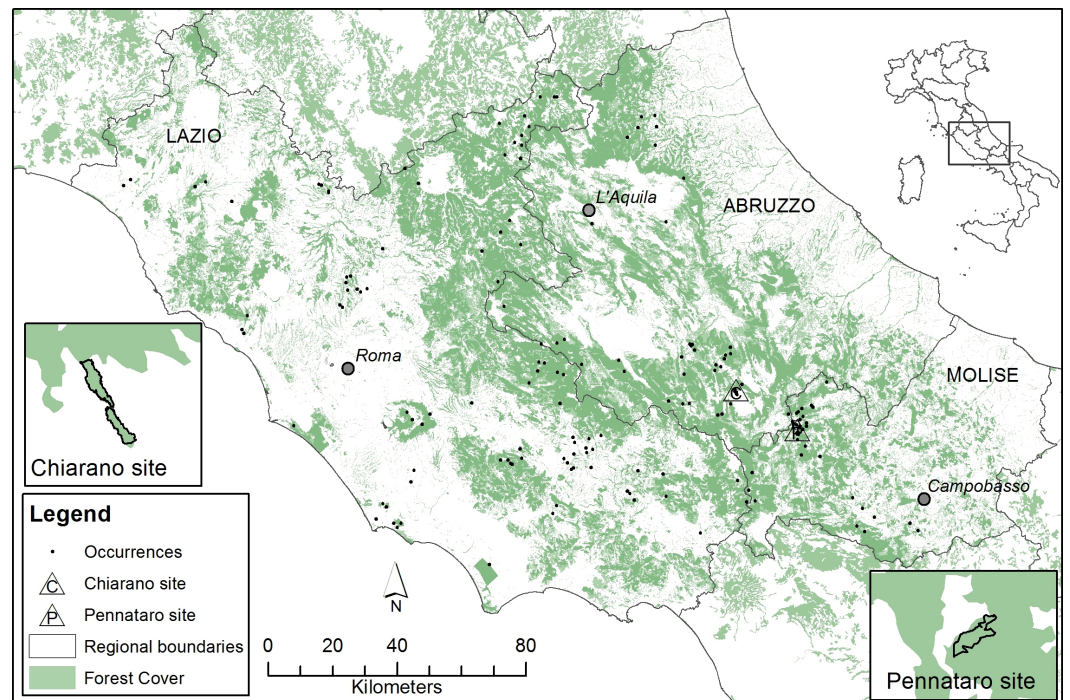
Figure 1 Treecreeper's occurrences used to build the distribution models. The study area is located in central-southern Italy, within Abruzzo, Lazio and Molise regions.

Table 1 Surface of the habitat types included in the analysis within the study area (Abruzzo, Lazione and Molise regions, central Italy) and number of short-toed treecreeper's occurrences.

Forests and tree plantations habitat types	Area (km²)	N° of treecreeper's occurrences
Holm oak (*Quercus ilex*)	511.9	8
Downy oak (*Q. pubescens*)	1986.3	13
Turkey oak (*Q. cerris*)	2412.3	51
Orno-ostryetum (mixed deciduous woodland with prevailing *Fraxinus ornus* and *Ostrya carpinifolia*)	1342.4	20
Chestnut (*Castanea sativa*)	628.1	10
Tilio-Acerion	0.12	0
Beech (*Fagus sylvatica*)	2360.4	40
Salix sp. and *Populus* sp. riparian woodlands and poplar plantations	536.5	12
Tree plantations and bushes	649.7	8
Conifer (both natural and reforestation)	545	4
Shrubland and maquis	1313.1	4
Non forest	20129.3	0

range and territory size of the short-toed treecreeper (*Cramp, 1988*). Accordingly, we chose to use the normalized difference vegetation index (NDVI) as a proxy of forest cover and structure, integrating it into the modelling framework. The NDVI is highly correlated with the leaf area index and the net primary productivity (*Myneni et al., 1995*; *Pettorelli et al., 2005*; *Lee et al., 2006*) and was calculated from Landsat 8 multispectral images, with 30 m

spatial resolution. NDVI was computed over a mosaic of five images with cloud cover <10%, collected between July and August 2013, which had undergone the atmospheric correction procedure. Finally, altitude was integrated through a digital elevation model (DEM) provided by the National Institute for Environmental Protection and Research (ISPRA), available at http://www.sinanet.isprambiente.it/it.

Spatial autocorrelations of the environmental predictors within occurrence points were tested through a Mantel test in order to detect any spatial autocorrelations among occurrences (Fig. S1). Analyses were carried out with the R package 'ecospat' (Broennimann, Di Cola & Guisan, 2016).

Among the eight selected algorithms, the maximum entropy (ME) used presence-only points in combination with background samples, using only quadratic and hinge features to avoid overfitting (Phillips, Anderson & Schapire, 2006; Elith et al., 2011). The other algorithms, which were supplied with pseudo-absences and true absences, were: an artificial neural network (ANN; Segurado & Araujo, 2004), classification tree analyses (CTA; Breiman et al., 1984; De'ath, 2002), flexible discriminant analyses (FDA; Hastie, Tibshirani & Buja, 1994), generalized boosting model (GBM; Friedman, 2001), generalized linear model (GLM; McCullagh & Nelder, 1989), multivariate additive regression spline (MARS; Moisen & Frescino, 2002) and random forest (RF; Breiman, 2001) (Table 2). Ten thousand absence points were sampled in the environmental background (Elith et al., 2006), comprising 975 points of actual absence derived from the MITO2000 database and 9025 pseudo-absences, randomly selected within the area where the logistic output of ME was less than 0.2 (Chefaoui & Lobo, 2008; Wisz & Guisan, 2009), representing an adequate number of pseudo-absences (Barbet-Massin et al., 2012). SDMs were trained using 70% of randomly selected occurrences, while the remaining 30% were used for testing; the procedure was iterated 30 times (except for ME with 50 iterations) (further details are provided in Table 2). The area under the curve (AUC) of the receiving operating characteristic (Hanley & McNeil, 1982) was used to evaluate the predictive power of the SDMs. To improve the readability of SDM outputs, sensitivity (i.e., the proportions of correct positive prediction) and specificity (i.e., the proportion of correct negative prediction) and the true skill statistic (TSS) were also reported (Allouche, Tsoar & Kadmon, 2006; Lobo, Jiménez-Valverde & Real, 2008). The importance of each environmental predictor was calculated following Thuiller et al. (2009). Analyses were carried out with the software MaxEnt (Phillips, Anderson & Schapire, 2006) and the biomod2 package integrated in R (Thuiller et al., 2009; R Development Core Team, 2015; Thuiller, Georges & Engler, 2015).

Abundance estimation

Abundance was estimated in two forest stands used as test sites of the LIFE+ ManFor C.BD: Bosco Pennataro Regional Forest and Chiarano-Sparvera Regional Forest. Bosco Pennataro (BP, 41°44′N, 14°11′E, 1,000 m a.s.l.) consists of a multi-layered high forest stand dominated by turkey oak (Quercus cerris). Chiarano-Sparvera (CS, 41°51′N, 13°57′E, 1,700 m a.s.l.) is a pure beech (Fagus sylvatica) forest, in transition from coppice to high forest. Following a systematic design, 27 and 23 sampling points, 125.5 m (±19.7 sd) away from one another, were selected in BP and CS, respectively. Surveys were carried out from

Table 2 Settings used for species distribution modelling and resulted AUC (area under the curve of the receiving operator characteristic), sensitivity, specificity and TSS (true skills statistic).

Full name	Acronym	Pseudo-absences	Parameters	AUC	Sensitivity	Specificity	TSS
Artificial neural network	ANN	10,000	5-fold cross validation	0.949	92.045	89.689	0.771
Classification tree analyses	CTA	10,000	5-fold cross validation	0.918	85.795	93.839	0.792
Flexible discriminant analyses	FDA	10,000	Default with MARS to increase predictive power	0.894	82.955	93.849	0.768
Generalized boosting model	GBM	10,000	5,000 maximum trees, 5 interaction and 10-fold cross validation	0.961	93.75	94.529	0.842
Generalized linear model	GLM	10,000	AIC-based stepwise model selection	0.959	93.182	91.159	0.835
Multivariate additive regression splines	MARS	10,000	Spline knots are determined automatically	0.913	89.205	89.129	0.782
Maximum entropy	ME	No; 10,000 background points	1,000 bootstrap iterations	0.929	–	–	–
Random forest	RF	10,000	750 trees, 10-fold cross validation	1	100	99.98	1

May to June (2012 in CS; 2013 in BP) from sunrise till 11:00 a.m. At every point, each individual detected by aural/visual cues during a five-minute count was recorded. Each point was visited two to six times (average = 3.4; total = 177).

Local abundance was estimated with N-mixture models (*Royle, 2004b*). This approach considers local abundance (i.e., abundance estimated in each sampling point) as an independent random point process (*Royle, 2004a*). Two separate models were built for BP and CS, respectively: with and without detectability variation among occasions. Model fit and overdispersion (also called c-hat) was tested through a Pearson χ^2 goodness-of-fit test, with 1,000 bootstrap resampling (*MacKenzie & Bailey, 2004*). Model selection proceeded through Akaike's Information Criterion, which assigns scores both to the likelihood of the model and the number of parameters included (*Burnham & Anderson, 2002*). Spatial dependence of estimates was assessed with the Moran test and index calculation (*Moran, 1950*). Analyses were carried out using the packages *unmarked* (*Fiske & Chandler, 2011*), *AICmodavg* (*Mazerolle, 2015*) and *spdep* (*Bivand & Piras, 2015*) implemented in R (*R Development Core Team, 2015*).

Statistical analyses

Local abundances (i.e., the abundance at every sampling point) in BP and CS were tested for differences with an *F*-test, followed by a *t*-test. Habitat suitability values, defined as the SDM outputs, were then extracted from a discrete area surrounding every abundance point. Width of the area in question was proportional to local abundance and was derived by

Basile et al. (2016), *PeerJ*, DOI 10.7717/peerj.2398

7/24

transforming the estimated population size (i.e., the sum of local abundances) into densities (ind./ha): the area of interest for density transformation was given by the minimum convex polygon among the sampling points. The difference between BP and CS environmental suitability values was tested by an F-test and a t-test. The landscape metric values were also tested for difference with the same methods.

The relationship between abundance and environmental suitability can form a triangular envelope, where increasing values of environmental suitability are matched by increasing values of the maximum abundance, not just the mean abundance (*VanDerWal et al., 2009*). Therefore, quantile regression can best provide the opportunity to explore the relation between environmental suitability and the upper quantiles of the abundance (*Cade, Noon & Flather, 2005*). The triangular envelope can predict maximum abundance, given a suitability value, due to the increase in the slope of regressions of upper quantiles, while intercepts remain similar (*VanDerWal et al., 2009*). However, two factors can mask the results: first, random variation at every point also due to local limiting factors that are not feasible to model; secondly, the spatial structure of the data, that can generate autocorrelation. Therefore, quantile mixed regressions were implemented to model the abundance as a function of HS values of every SDM, with a null random term and a grouping factor identifying the two locations. The random effect is estimated through best linear prediction (*Geraci & Bottai, 2013*). Model fit was assessed for every quantile through comparison of AIC scores with the null model of the corresponding quantile (*Burnham & Anderson, 2002*). Statistical analysis was carried out with the *lqmm* package (*Geraci, 2014*) in R (*R Development Core Team, 2015*).

RESULTS

Each SDM showed an AUC > 0.9, except for FDA (Table 2). Among them, RF ranked the highest value (AUC = 1). However, the geographical projections of the SDMs proved dissimilar (see Fig. S2). The importance of each environmental predictor had the same pattern for every algorithm, with forest type and NDVI proving the most important (Fig. 2). The importance of the three landscape metrics (H, AI, ED) indicates that the spatial configuration of landscape structures exerts a major influence on potential distribution.

Abundance models that performed best in both study areas were those in which detectability was invariant between sessions. Detectability was 0.34 ($\pm$0.11 SE) in Bosco Pennataro and 0.21 ($\pm$0.27 SE) in Chiarano Sparvera. Local abundances significantly differed between the two areas ($F = 0.77$, $p = 0.53$; $t = -3.57$, $p < 0.001$), and mean estimates were 1.54 ($\pm$0.52 SE) in BP and 0.86 ($\pm$1 SE) individuals/point in CS. Both models returned a good fit, with no overdispersion (BP: $\chi^2 = 64.3$, $p = 0.997$, c-hat = 0.687; CS: $\chi^2 = 52.5$, $p = 0.391$, c-hat = 1). Estimates did not show spatial autocorrelation in the two forest stands, obtaining a Moran I of 0.11 ($p = 0.14$) and -0.26 ($p = 0.92$) for BP and CS, respectively.

Habitat suitability also proved different between BP and CS, for every SDM (Table 3), and HS was higher in BP. In parallel, the values of landscape metrics significantly differed between the two forest stands except for edge density (Table 3). Specifically, Bosco Pennataro landscape structure resulted in larger and less scattered patches (AI = 98),
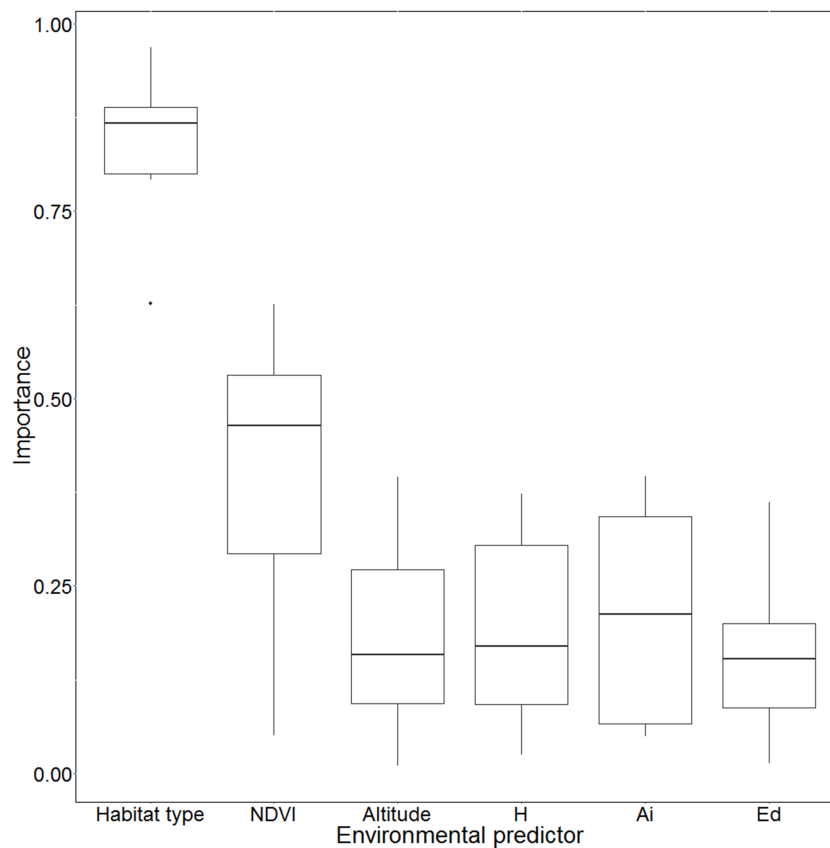
Figure 2 Variable importance based on different Species Distribution Models (SDMs). NDVI, Normalized difference vegetation index; H', Shannon index computed on landscape patch type diversity; Ai, aggregation index of landscape patches; Ed, patches' edge density.

equally distributed among types (H' = 0.93), compared to CS (AI = 92.6; H' = 0.76). Hence, landscape metrics showed a more fragmented landscape in CS than in BP, as expected.

Quantile regression showed a positive relationship between abundance and HS (Fig. 3 and Fig. S3). No differences emerged for the regression slope of each quantile, while intercept values proved more variable. Moreover, the majority of slopes were not significant except for CTA, GBM and GLM (see Table S1), even if AIC comparison indicated that most of the quantiles performed better than the corresponding null model (Table 4).

DISCUSSION

We examined the abundance and habitat suitability resulting from many algorithms for species distribution modelling (*Elith et al., 2006*; *Li & Wang, 2013*) of a forest-dwelling passerine in a region with different degrees of fragmentation. Although SDMs showed high AUCs, geographical projections varied quite substantially among algorithms, even if their explanatory variables followed the same pattern of importance scoring. Moreover, AUC computation for ME differs from the other algorithms, which made use of (pseudo) absences, being not comparable (*Yackulic et al., 2013*). Several studies that compared SDM

Table 3 Test for differences of landscape metrics and environmental suitability between Bosco Pennataro and Chiarano-Sparvera, based on Species Distribution Models (SDMs).

	F	*P*	*t*	*p*
Metric				
H'	0.065	0.000	3.3342	0.0027
Ed	0.3583	0.0134	−1.5038	0.1392
Ai	0.221	0.000	7.1504	0.000
Model				
ANN	0.07	0.000	−36	0.000
CTA	4.901	0.000	−9.93	0.000
FDA	2433.4	0.000	−8.06	0.000
GBM	1.137	0.748	−10.91	0.000
GLM	2.996	0.008	−2.949	0.002
MARS	14648	0.000	−4.893	0.000
ME	46.35	0.000	−4.682	0.000
RF	30.42	0.000	−4.044	0.000

Notes.
H', Shannon index of patch type diversity; Ed, edge density; Ai, aggregation index; F, Fisher's test; t, t test; P, p value; model abbreviation are given in Table 2.

Table 4 DeltaAIC between null model and suitability-dependant model, for the same quantile.

Quantile	ANN	CTA	FDA	GBM	GLM	MARS	ME	RF
0.5	0	0	0	0	0	0	0	0.50
0.55	0	0	0	0	0	0	0	1.20
0.6	0	0	0	0	0	0	0	1.39
0.65	0	0	0	0	2.88	0	0	1.86
0.7	0	0	0	0	0	0	0.17	0.93
0.75	0	0	0	0	0	0	0	0
0.8	0	0	0	0	4.67	23.93	0	0
0.85	25.74	0	0	0	2.17	7.79	6.29	9.14
0.9	0	31.93	1.15	26.85	0	23.91	2.98	3.07
0.95	44.78	16.49	3.38	0	15.94	6.83	4.35	0
0.975	32.65	0	0	0	0	31.32	0	0
0.99	0	0	0	0	0	0	0	1.69

outputs differed substantially (*Segurado & Araujo, 2004*; *Elith et al., 2006*; *Moisen et al., 2006*; *Meynard & Quinn, 2007*). Among those that based their comparison on AUC, ANN was favoured over CTA and GLM (*Segurado & Araujo, 2004*) and GBM and ME were favoured over MARS and GLM (*Elith et al., 2006*). GBM and GLM were preferred to CTA also by other authors (*Moisen et al., 2006*; *Meynard & Quinn, 2007*). What emerged from the literature is that complex models usually outperform simple models, especially when they involve specialist species (*Jiménez-Valverde, Lobo & Hortal, 2008*; *Li & Wang, 2013*). Indeed, our results are not totally concordant with findings elsewhere, simple models like GLM and GBM having scored higher AUC values. However, the use of AUC has been criticised by many authors even if there are currently no consensus methods to assess the
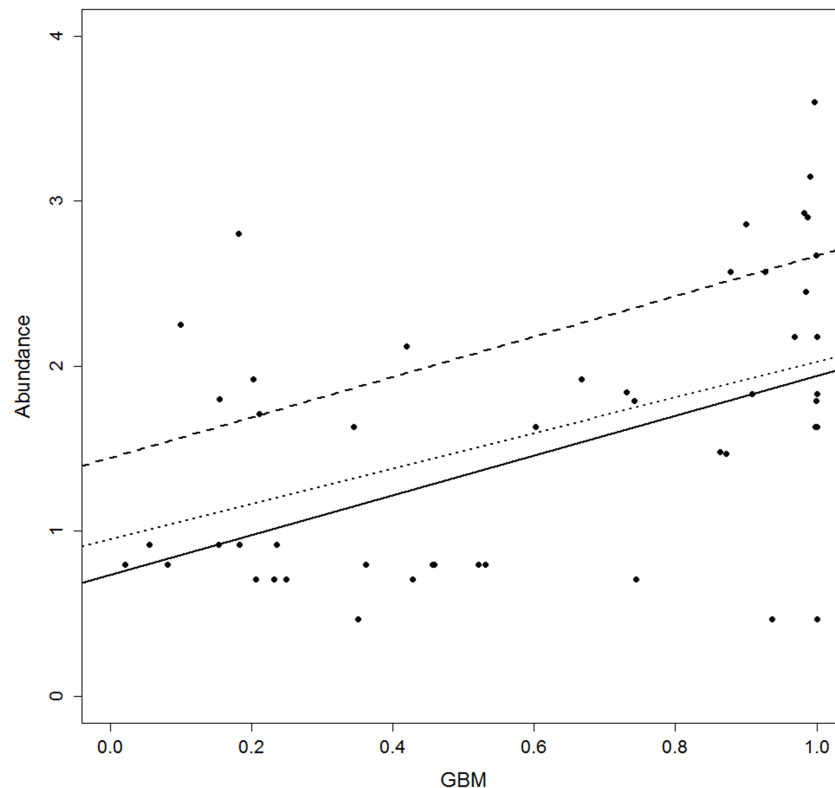
Figure 3 **Scatterplot of abundance versus habitat suitability (as predicted by the Generalised Boosting model, GBM).** Regression lines represent the fitted relationship at different quantiles. Quantiles: solid line = 0.5 quantile, slope = 0.37, $p < 0.5$; dashed line = 0.75, slope = 0.19, p = n.s.; dotted line = 0.95, slope = 0.13, p = n.s.

predictability of SDMs (*Austin, 2007*; *Lobo, Jiménez-Valverde & Real, 2008*). Specifically, the AUC does not consider the goodness of fit of a model and it is higher when more pseudo-absences in unsuitable localities are included in the model (*Lobo, Jiménez-Valverde & Real, 2008*). Nevertheless, its use is still widespread (*Elith & Graham, 2009*; *Barbet-Massin et al., 2012*). It should also be pointed out that, even if we used a large number of (pseudo) absences, we also employed a larger number of presence points than what is usually found in the literature (e.g., *Pearson et al., 2007*).

SDM output can usually be considered as a probability of occurrence, somewhat related to habitat suitability (*Franklin, 2009*). In the case of ME, this is achieved after logistic transformation (*Phillips & Dudík, 2008*). This approach has been criticised because of the frequent violation of two major assumptions: randomness of the samples and constant detectability among individuals (*Royle et al., 2012*; *Merow, Smith & Silander, 2013*). Indeed, the logistic output uses a rather subjective intercept of 0.5, which is valid, though its reliability is not proven (*Royle et al., 2012*). Use of pseudo-absence also needs caution, since the background in which sampling takes place has both suitable and unsuitable locations (*Pearce & Boyce, 2006*). However, we employed an analytical framework designed to reduce this source of bias. The randomness of the presence points is due to the use of occurrences coming from a standardised monitoring programme. For the same reasons, we

assume that the variability in detectability is reduced to the minimum, demonstrating this issue also in the two forests where we estimated abundance (i.e., BP and CS). Finally, our use of the logistic output of ME, as well as of its subjective intercept of 0.5, is based upon the consideration that 37% of the study area is covered in forest. Therefore, assuming an intercept of 0.5 does not seem too far from reality scenario. Indeed, ME has been proved to be one of the most reliable SDMs when only presence data are available (*Franklin, 2009*; *Merow, Smith & Silander, 2013*). Our use of ME, moreover, was functional to the selection of pseudo-absences, which were not selected within the entire region, but only in a restricted area considered unsuitable by ME. As a consequence, we also assume that our method of selecting pseudo-absence greatly reduced an eventual bias. At the very end, we considered SDM outputs as a habitat suitability index, which we could assume to be related to actual environmental suitability (*VanDerWal et al., 2009*; *Brambilla & Ficetola, 2012*).

For reliable modelling, it is necessary to use ecologically relevant environmental predictors (*Austin, 2007*), even if it is not possible to include every environmental variable thought to affect the distribution of a species (*Elith & Leathwick, 2009*). We based the choice of environmental variables on both the known species-habitat relationships and on the possibility of obtaining relevant information to steer management, relying on forest type, structure, productivity and fragmentation. Forest type and NDVI proved the most important variables in predicting the distribution of the short-toed treecreeper. The NDVI is not only positively correlated to net primary productivity (*Myneni et al., 1995*; *Pettorelli et al., 2005*), but also to the structural complexity of forests (*Manes et al., 2010*). As a consequence, among the same forest type, a higher NDVI is related, given that all other variables are comparable, to more structured, multi-layered forests or to forest patches that are more productive or that have a higher leaf area index, where specialist birds can find a more suitable habitat (*Newton, 1994*; *Carrillo-Rubio et al., 2014*). Obviously, this conclusion also depends on the patch size and the degree of fragmentation, which are intertwined with NDVI and forest type. Indeed, a substantial influence of landscape structure in defining habitat suitability was clearly apparent when taking into account the three metrics together. Responses to fragmentation are species-specific and, usually, the more specialist a species, the more negative its response (*Devictor, Julliard & Jiguet, 2008*; *Rueda et al., 2013*). SDM outputs showed higher HS in localities in less fragmented landscapes, in agreement with the literature on forest specialist birds (*Fahrig, 2003*).

We used hierarchical statistical analysis of abundance to obtain unbiased estimates, corrected for detectability (*Royle, 2004a*). The significant difference in abundances between Bosco Pennataro and Chiarano-Sparvera is matched by the difference in the suitability of the two forests. Therefore, differences in abundance, HS and landscape metrics matched the same pattern: in locations with more degraded forest, both HS and abundance scored lower values, even though abundance showed higher variability, confounding the hypothesised relationships with HS.

Our results suggest that there is a positive relationship between habitat suitability and treecreeper abundance, even if the hypothesised triangular envelope (*VanDerWal et al., 2009*) did not emerge. However, its predictive power was quite weak, due to high abundance variability in both low and high HS locations. Extensive research has yielded little evidence

for the relationship between demographic parameters and HS (*Pearce & Ferrier, 2001*; *Nielsen et al., 2005*; *Jiménez-Valverde et al., 2009*). Related findings are often discordant (*Jiménez-Valverde et al., 2009*; *Tôrres et al., 2012*) and many concerns are raised on the controversial and often unconfirmed empirical relationships between ecological processes and landscape patterns (*Turner, Gardner & O'Neill, 2001*; *Kupfer, 2012*). That said, the relationship can be masked by the many unmodelled environmental variables that can conceal local suitability (*Lobo, Jiménez-Valverde & Real, 2008*). For this reason, *VanDerWal et al. (2009)* concluded that just the upper limit of abundance, and not its mean value, is predictable from HS. However, this relationship has been widely found to be very weak due to the difficulty to obtain reliable estimates of both abundance and HS (*Jiménez-Valverde, 2011*; *Oliver et al., 2012*; *Tôrres et al., 2012*). Some exceptions are presumably due to the use of indexes of abundance, instead of actual estimates (*De Moraes Weber & Viveiros Grelle, 2012*; *Gutiérrez et al., 2013*). Indeed, our approach was based not only on abundance estimates but also on HS values from different algorithms and averaged over the likely home range size. Moreover, our use of landscape features as predictive variables could have enhanced model performance since other studies (e.g., *Tôrres et al., 2012*), based mostly on climatic variables, found positive but weaker relationships between HS and abundance.

This result, though confirming the existence of a relationship, also highlights the limits of the SDM approach, suggesting that low HS can also occur in areas of high abundance, probably due to environmental factors that are not considered in modelling which may increase the actual HS of the area.

CONCLUSION

Birds are considered good biodiversity indicators, especially to monitor habitat alteration (e.g., fragmentation) (*Gregory et al., 2008*; *Carrillo-Rubio et al., 2014*; *Czeszczewik et al., 2014*). For instance, in the context of biotic homogenization, one likely effect is the disappearance of specialist species which are more closely associated to unaltered forests (*McKinney & Lockwood, 1999*). Negative effects of habitat alteration can persist over years (*Kendrick et al., 2014*). Thus identification of the main species-habitat relationships is important to prevent the disappearance of more susceptible species (*Villard, Trzcinski & Merriam, 1999*; *King & DeGraaf, 2000*). Further, fragmentation can cause the disappearance of the specialist component of biodiversity (*Fahrig, 2003*). Such processes can alter biological, ecological and demographic traits like brood survival and growth (*Suorsa et al., 2003*; *Le Tortorec et al., 2012*), occupancy or population size (*Schmiegelow, Machtans & Hannon, 1997*; *Villard, Trzcinski & Merriam, 1999*; *Cooper & Walters, 2002*). Through SDMs, such results can be transposed into geographic projection and inform conservationists and practitioners (*Ferrier et al., 2007*; *Maiorano et al., 2015*). Therefore, modelling how fragmentation can affect the distribution of a species and understand the eventual relations with population decrease, can greatly improve conservation and management plans.

A forest landscape is, in most European cases, a human-modified landscape whose properties, like patch size, can affect many species (*Gil-Tena, Torras & Saura, 2008*). Our approach takes into account such issues in order to provide information-based advice.

In this way, we define the relationships between a species and some "directly adjustable" landscape features. The Chiarano-Sparvera forest stand is naturally located in a more fragmented landscape than is Bosco Pennataro. Hence, the abundance response (i.e., decrease) of the short-toed treecreeper is matched by habitat choice. Fragmentation, extensive rejuvenation of forest stands and tree plantations are all factors that can contribute to alter the suitability of an area. Since habitat alteration can decrease species abundance sooner than effectively reducing their geographic range (*Shoo, Williams & Hero, 2005*), identification of areas of low HS, where impact on abundance is more likely to cause local extinctions, could act as an early warning for species conservation. In our approach, these threats can occur on a large scale, can be related to possible changes in abundance and then used to inform practitioners and managers. Moreover, prediction of future land use scenarios can be implemented.

However, our results are a case study, limited to a single specialist species, strictly linked to mature well-preserved forests. This approach could be extended over different kinds of habitats and species, other than forests. Moreover, the modelling should be refined to include other potential resources and limiting factors, whether biotic or abiotic, in order to obtain more robust HS prediction (*Guisan & Thuiller, 2005*). The magnitude of the relationship between HS and abundance can then be used as a form of model validation (*Lobo, Jiménez-Valverde & Real, 2008*), thus helping to steer sound land use management and conservation planning.

ACKNOWLEDGEMENTS

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Grant Disclosures

REFERENCES

Allouche O, Tsoar A, Kadmon R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**:1223–1232 DOI 10.1111/j.1365-2664.2006.01214.x.

Austin M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* **200**:1–19 DOI 10.1016/j.ecolmodel.2006.07.005.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**:327–338 DOI 10.1111/j.2041-210X.2011.00172.x.

Bearer S, Linderman M, Huang J, An L, He G, Liu J. 2008. Effects of fuelwood collection and timber harvesting on giant panda habitat use. *Biological Conservation* **141**:385–393 DOI 10.1016/j.biocon.2007.10.009.

Bender DJ, Tischendorf L, Fahrig L. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* **18**:17–39 DOI 10.1023/A:1022937226820.

BirdLife International. 2016. *Certhia brachydactyla.* IUCN Red List for birds. *Available at* http://www.birdlife.org/datazone/userfiles/file/Species/erlob/summarypdfs/22711249_certhia_brachydactyla.pdf.

Bivand R, Piras G. 2015. Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software* **63(18)**:1–36.

Blondel J, Ferry C, Frochot B. 1981. Point counts with unlimited distance. In: Ralph JC, Scott JM, eds. *Estimating numbers of terrestrial birds.* Asilomar: Studies in Avian Biology, 414–420.

Brambilla M, Ficetola GF. 2012. Species distribution models as a tool to estimate reproductive parameters: a case study with a passerine bird species. *Journal of Animal Ecology* **81**:781–787 DOI 10.1111/j.1365-2656.2012.01970.x.

Breiman L. 2001. Random forests. *Machine Learning* **45**:5–32 DOI 10.1023/A:1010933404324.

Breiman L, Friedman JH, Olshen RA, Stone CJ. 1984. *Classification and regression tree.* Belmont: Wadsworth International Group.

Broennimann O, Di Cola V, Guisan A. 2016. ecospat: spatial ecology miscellaneous methods. R package V 2.0. *Available at* https://cran.r-project.org/web/packages/ecospat/.

Burnham KP, Anderson DR. 2002. *Model selection and multimodal inference.* New York: Springer-Verlag.

Cade BS, Noon BR, Flather CH. 2005. Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology* **86**:786–800 DOI 10.1890/04-0785.

Calladine J, Bray J, Broome A, Fuller RJ. 2015. Comparison of breeding bird assemblages in conifer plantations managed by continuous cover forestry and clearfelling. *Forest Ecology and Management* **344**:20–29 DOI 10.1016/j.foreco.2015.02.017.

Carrillo-Rubio E, Kéry M, Morreale SJ, Sullivan PJ, Gardner B, Cooch EG, Lassoie JP. 2014. Use of multispecies occupancy models to evaluate the response of bird communities to forest degradation associated with logging. *Conservation Biology* **28**:1034–44 DOI 10.1111/cobi.12261.

Chefaoui RM, Assis J, Duarte CM, Serrão EA. 2015. Large-scale prediction of seagrass distribution integrating landscape metrics and environmental factors: the case of Cymodocea nodosa (Mediterranean–Atlantic). *Estuaries and Coasts* **39(1)**:123–127 DOI 10.1007/s12237-015-9966-y.

Chefaoui RM, Lobo JM. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling* **210**:478–486 DOI 10.1016/j.ecolmodel.2007.08.010.

Cody ML. 1985. *Habitat selection in birds.* Orlando: Academic Press.

Cooper CB, Walters JR. 2002. Independent effects of woodland loss and fragmentation on Brown Treecreeper distribution. *Biological Conservation* **105**:1–10.

Craig MD. 2007. The short-term effects of edges created by forestry operations on the bird community of the jarrah forest, south-western Australia. *Austral Ecology* **32**:386–396 DOI 10.1111/j.1442-9993.2007.01710.x.

Cramp S (ed.) 1988. *The birds of the Western Peleartic.* Oxford: Oxford University Press.

Czeszczewik D, Zub K, Stanski T, Sahel M, Kapusta A, Walankiewicz W. 2014. Effects of forest management on bird assemblages in the Bialowieza Forest, Poland. *iForest—Biogeosciences and Forestry* **8(3)**:377–385 DOI 10.3832/ifor1212-007.

Darvishi A, Fakheran S, Soffianian A. 2015. Monitoring landscape changes in Caucasian black grouse (Tetrao mlokosiewiczi) habitat in Iran during the last two decades. *Environmental Monitoring and Assessment* **187**:443 DOI 10.1007/s10661-015-4659-3.

De Moraes Weber M, Viveiros Grelle CE. 2012. Does environmental suitability explain the relative abundance of the tailed tailless bat, Anoura caudifer? *Natureza and Conservaçao* **10**:221–227 DOI 10.4322/natcon.2012.035.

De'ath G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* **83**:1105–1117 DOI 10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2.

Devictor V, Julliard R, Jiguet F. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **117**:507–514 DOI 10.1111/j.0030-1299.2008.16215.x.

Donald PF, Fuller RJ, Evans AD, Gough SJ. 1998. Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. *Biological Conservation* **85**:183–197 DOI 10.1016/S0006-3207(97)00114-6.

Elith J, Graham CH. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* **32**:66–77 DOI 10.1111/j.1600-0587.2008.05505.x.

Elith J, Graham CH, Anderson RP, Dudik 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 JMC, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**:129–151 DOI 10.1111/j.2006.0906-7590.04596.x.

Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677–697 DOI 10.1146/annurev.ecolsys.110308.120159.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**:43–57 DOI 10.1111/j.1472-4642.2010.00725.x.

Escobar MAH, Uribe SV, Chiappe R, Estades CF. 2015. Effect of clearcutting operations on the survival rate of a small mammal. *PLoS ONE* **10**:e0118883 DOI 10.1371/journal.pone.0118883.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**:487–515 DOI 10.1146/annurev.ecolsys.34.011802.132419.

Farashi A, Kaboli M, Karami M. 2013. Predicting range expansion of invasive raccoons in northern Iran using ENFA model at two different scales. *Ecological Informatics* **15**:96–102 DOI 10.1016/j.ecoinf.2013.01.001.

Ferrier S, Manion G, Elith J, Richardson K. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions* **13**:252–264 DOI 10.1111/j.1472-4642.2007.00341.x.

Fiske IJ, Chandler RB. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* **43**:1–23 DOI 10.18637/jss.v043.i10.

Fornasari L, Londi G, Buvoli L, Tellini Florenzano G, La Gioia G, Pedrini P, Brichetti P, De Carli E. 2010. Distribuzione geografica e ambientale degli uccelli comuni nidificanti in Italia, 2000–2004 (dati del progetto MITO2000). *Avocetta* **34**:5–224.

Franklin J. 2009. *Mapping species distributions: spatial inference and prediction.* Cambridge: Cambridge University Press.

Friedman JH. 2001. Greedy function approximation: a gradient boosting machine. *The Annals of Statistics* **29**:1189–1232 DOI 10.1214/aos/1013203451.

Garfí V, Marchetti M. 2011. *Tipi forestali e preforestali della regione Molise.* Alessandria: Edizioni dell'Orso S.r.l.

Geraci M. 2014. Linear quantile mixed models: the lqmm package for laplace quantile regression. *Journal of Statistical Software* **57**:1–29 DOI 10.18637/jss.v057.i13.

Geraci M, Bottai M. 2013. Linear quantile mixed models. *Statistics and Computing* **24**:461–479 DOI 10.1007/s11222-013-9381-9.

Gil-Tena A, Torras O, Saura S. 2008. Relationship between forest landscape structure and avian species richness in NE Spain. *Ardeola* **55**:27–40.

Gregory RD, Voříšek P, Noble DG, Van Strien A, Klvaňová A, Eaton M, Gmelig Meyling AW, Joys A, Foppen RPB, Burfield IJ. 2008. The generation and use of bird population indicators in Europe. *Bird Conservation International* **18**:223–244 DOI 10.1017/S0959270908000312.

Grinnell J. 1917. The niche-relationships of the California thrasher. *The Auk* **34**:427–433 DOI 10.2307/4072271.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**:993–1009 DOI 10.1111/j.1461-0248.2005.00792.x.

Gutiérrez D, Harcourt J, Díez SB, Illán JG, Wilson RJ. 2013. Models of presence-absence estimate abundance as well as (or even better than) models of abundance: the case of the butterfly Parnassius apollo. *Landscape Ecology* **28**:401–413 DOI 10.1007/s10980-013-9847-3.

Hanley J, McNeil B. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* **143**:29–36 DOI 10.1148/radiology.143.1.7063747.

Hastie T, Tibshirani R, Buja A. 1994. Flexible discriminant analysis by optimal scoring. *Journal of the American Statistical Association* **89**:1255–1270 DOI 10.1080/01621459.1994.10476866.

He HS, Dezonia BE, Mladenoff DJ. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. *Landscape Ecology* **15**:591–601 DOI 10.1023/A:1008102521322.

Holt RD. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America* **106**:19659–19665 DOI 10.1073/pnas.0905137106.

Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**:415–427 DOI 10.1101/SQB.1957.022.01.039.

Jackson ST, Overpeck JT. 2000. Responses of plant populations and communities to environmental changes of the late quaternary. *Paleobiology* **26**:194–220 DOI 10.1666/0094-8373(2000)26[194:ROPPAC]2.0.CO;2.

Jiménez-Valverde A. 2011. Relationship between local population density and environmental suitability estimated from occurrence data. *Frontiers of Biogeography* **3.2**:59–61.

Jiménez-Valverde A, Diniz F, De Azevedo EB, Borges PAV. 2009. Species distribution models do not account for abundance: the case of arthropods on Terceira Island. *Annales Zoologici Fennici* **46**:451–464 DOI 10.5735/086.046.0606.

Jiménez-Valverde A, Lobo JM, Hortal J. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions* **14**:885–890 DOI 10.1111/j.1472-4642.2008.00496.x.

Kendrick SW, Porneluzi PA, Thompson III FR, Morris DL, Haslerig JM, Faaborg J. 2014. Stand-level bird response to experimental forest management in the Missouri Ozarks. *The Journal of Wildlife Management* **79**:50–59 DOI 10.1002/jwmg.804.

King DI, DeGraaf RM. 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. *Forest Ecology and Management* **129**:227–235 DOI 10.1016/S0378-1127(99)00167-X.

Kumar S, Stohlgren TJ, Chong GW. 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* **87**:3186–3199 DOI 10.1890/0012-9658(2006)87[3186:SHINAN]2.0.CO;2.

Kupfer JA. 2012. Landscape ecology and biogeography: rethinking landscape metrics in a post-FRAGSTATS landscape. *Progress in Physical Geography* **36**:400–420 DOI 10.1177/0309133312439594.

Le Tortorec E, Helle S, Suorsa P, Sirkiä P, Huhta E, Nivala V, Hakkarainen H. 2012. Feather growth bars as a biomarker of habitat fragmentation in the Eurasian treecreeper. *Ecological Indicators* **15**:72–75 DOI 10.1016/j.ecolind.2011.09.013.

Lee KS, Park YI, Kim SH, Park JH, Woo CS, Jang KC. 2006. Remote sensing estimation of forest LAI in close canopy situation. *Korean Journal of Remote Sensing* **22**:305–311.

Li X, Wang Y. 2013. Applying various algorithms for species distribution modelling. *Integrative Zoology* **8**:124–135 DOI 10.1111/1749-4877.12000.

Lobo JM, Jiménez-Valverde A, Real R. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**:145–151 DOI 10.1111/j.1466-8238.2007.00358.x.

Loehle C, Wigley TB, Rutzrnoser S, Gerwin JA, Keyser PD, Lancia RA, Reynolds CJ, Thill RE, Weih R, White DJ, Wood PB. 2005. Managed forest landscape structure and avian species richness in the southeastern US. *Forest Ecology and Management* **214**:279–293 DOI 10.1016/j.foreco.2005.04.018.

MacArthur R, Recher H, Cody M. 1966. On the relation between habitat selection and species diversity. *The American Naturalist* **100**:319–332 DOI 10.1086/282425.

MacKenzie DI, Bailey LL. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* **9**:300–318 DOI 10.1198/108571104X3361.

Maiorano L, Boitani L, Monaco A, Tosoni E, Ciucci P. 2015. Modeling the distribution of Apennine brown bears during hyperphagia to reduce the impact of wild boar hunting. *European Journal of Wildlife Research* **61**(**2**):241–253 DOI 10.1007/s10344-014-0894-0.

Manes F, Ricotta C, Salvatori E, Bajocco S, Blasi C. 2010. A multiscale analysis of canopy structure in *Fagus sylvatica L.* and *Quercus cerris L.* old-growth forests in the Cilento and Vallo di Diano National Park. *Plant Biosystems* **144**:202–210 DOI 10.1080/11263500903560801.

Marchetti M, Chiavetta U, Santopuoli G. 2009. La cartografia forestale su base tipologica della Regione Abruzzo: dai "prodromi" alla carta forestale dell'Italia centrale. In: Collalti D, D'Alessandro L, Marchetti M, Sebastiani A, eds. *La carta tipologico-forestale della Regione Abruzzo.* L'Aquila: Regione Abruzzo, 13–29.

Martínez-Meyer E, Díaz-Porras D, Peterson AT, Yáñez-Arenas CY. 2013. Ecological niche structure and rangewide abundance patterns of species. *Biology Letters* **9**:20120637 DOI 10.1098/rsbl.2012.0637.

Marvier M, Kareiva P, Neubert MG. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis* **24**:869–879 DOI 10.1111/j.0272-4332.2004.00485.x.

Mazerolle MJ. 2015. AICcmodavg. R package v. 2.0-3. *Available at https://cran.r-project.org/web/packages/AICcmodavg/index.html*.

McCullagh P, Nelder JA. 1989. *Generalized linear models.* London: Chapman and Hall.

McGarigal K, Cushman SA, Ene E. 2012. Fragstats v4: spatial pattern analysis program for categorical and continuous maps. *Available at http://www.umass.edu/landeco/research/fragstats/fragstats.html*.

McKinney ML, Lockwood JL. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**:450–453 DOI 10.1016/S0169-5347(99)01679-1.

Merow C, Smith MJ, Silander JA. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**:1058–1069 DOI 10.1111/j.1600-0587.2013.07872.x.

Meynard CN, Quinn JF. 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography* **34**:1455–1469 DOI 10.1111/j.1365-2699.2007.01720.x.

Moisen GG, Freeman EA, Blackard JA, Frescino TS, Zimmermann NE, Edwards TC. 2006. Predicting tree species presence and basal area in Utah: a comparison of stochastic gradient boosting, generalized additive models, and tree-based methods. *Ecological Modelling* **199**:176–187 DOI 10.1016/j.ecolmodel.2006.05.021.

Moisen GG, Frescino TS. 2002. Comparing five modelling techniques for prediction forest characteristics. *Ecological Modelling* **157**:209–225 DOI 10.1016/S0304-3800(02)00197-7.

Moran PAP. 1950. Notes on continuous stochastic phenomena. *Biometrika* **37**:17–23 DOI 10.1093/biomet/37.1-2.17.

Morand S, Bordes F, Blasdell K, Pilosof S, Cornu J-F, Chaisiri K, Chaval Y, Cosson JF, Claude J, Feyfant T, Herbreteau V, Dupuy S, Tran A. 2015. Assessing the distribution of disease-bearing rodents in human-modified tropical landscapes. *Journal of Applied Ecology* **52**:784–794 DOI 10.1111/1365-2664.12414.

Myneni RB, Hall FG, Sellers PJ, Marshak AL. 1995. The interpretation of spectral vegetation indexes. *Transactions on Geoscience and Remote Sensing* **33**:481–486 DOI 10.1109/36.377948.

Newton I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* **70**:265–276 DOI 10.1016/0006-3207(94)90172-4.

Nielsen SE, Johnson CJ, Heard DC, Boyce MS. 2005. Can models of presence-absence be used to scale abundance? Two studies considering extremes in life history. *Ecography* **28**:197–208 DOI 10.1111/j.0906-7590.2005.04002.x.

Nixon K, Silbernagel J, Price J, Miller N, Swaty R. 2014. Habitat availability for multiple avian species under modeled alternative conservation scenarios in the Two Hearted River watershed in Michigan, USA. *Journal for Nature Conservation* **22**:302–317 DOI 10.1016/j.jnc.2014.02.005.

Oliver TH, Gillings S, Girardello M, Rapacciuolo G, Brereton TM, Siriwardena GM, Roy DB, Pywell R, Fuller RJ. 2012. Population density but not stability can be predicted from species distribution models. *Journal of Applied Ecology* **49**:581–590 DOI 10.1111/j.1365-2664.2012.02138.x.

Open Data Lazio. 2012. Carta Forestale su base tipologica della Regione Lazio derivata dalla Carta delle formazioni naturali e seminaturali mediante approfondimento a IV e V livello Corine Land Cover della Carta dell'Uso del Suolo della Regione Lazio. *Agenzia Regionale Parchi—Regione Lazio, Rome, Italy. Available at http://dati.lazio.it/catalog/dataset/carta-forestale-su-base-tipologica-della-regione-lazio.*

Pearce JL, Boyce MS. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* **43**:405–412 DOI 10.1111/j.1365-2664.2005.01112.x.

Pearce J, Ferrier S. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation* **98**:33–43 DOI 10.1016/S0006-3207(00)00139-7.

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. *Journal of Biogeography* **34**:102–117 DOI 10.1111/j.1365-2699.2006.01594.x.

Penman, Mahony, Lemckert. 2005. Soil disturbance in integrated logging operations and the potential impacts on a fossorial Australian frog. *Applied Herpetology* **2**:415–424 DOI 10.1163/157075405774483111.

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to asses ecological responses to environmental change. *Trends in Ecology and Evolution* **20**:503–510 DOI 10.1016/j.tree.2005.05.011.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**:231–259 DOI 10.1016/j.ecolmodel.2005.03.026.

Phillips SJ, Dudík M. 2008. Modeling of species distribution with Maxent: new extensions and a comprehensive evalutation. *Ecograpy* **31**:161–175 DOI 10.1111/j.0906-7590.2008.5203.x.

R Development Core Team. 2015. R: a language and environment for statistical computing. Version 3.0.1. Vienna: R Project for Statistical Computing. *Available at https://www.r-project.org*.

Royle JA. 2004a. Generalized estimators of avian abundance from count survey data. *Animal Biodiversity and Conservation* **27**:375–386.

Royle JA. 2004b. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**:108–115 DOI 10.1111/j.0006-341X.2004.00142.x.

Royle JA, Chandler RB, Yackulic C, Nichols JD. 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution* **3**:545–554 DOI 10.1111/j.2041-210X.2011.00182.x.

Rueda M, Hawkins BA, Morales-Castilla I, Vidanes RM, Ferrero M, Rodríguez MÁ. 2013. Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds. *Global Ecology and Biogeography* **22**:1282–1292 DOI 10.1111/geb.12079.

Ryberg WA, Hill MT, Painter CW, Fitzgerald LA. 2013. Landscape pattern determines neighborhood size and structure within a lizard population. *PLoS ONE* **8**:e56856 DOI 10.1371/journal.pone.0056856.

Schindler S, Von Wehrden H, Poirazidis K, Wrbka T, Kati V. 2013. Multiscale performance of landscape metrics as indicators of species richness of plants, insects and vertebrates. *Ecological Indicators* **31**:41–48 DOI 10.1016/j.ecolind.2012.04.012.

Schmiegelow FKA, Machtans CS, Hannon SJ. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914–1932 DOI 10.1890/0012-9658(1997)078[1914:ABBRTF]2.0.CO;2.

Segurado P, Araujo MB. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* **31**:1555–1568 DOI 10.1111/j.1365-2699.2004.01076.x.

Shannon CE, Wiener W. 1949. *The mathematical theory of communication.* Urbana: University of Illinois Press.

Shifley SR, Thompson FR, Dijak WD, Fan Z. 2008. Forecasting landscape-scale, cumulative effects of forest management on vegetation and wildlife habitat: a case study of issues, limitations, and opportunities. *Forest Ecology and Management* **254**:474–483 DOI 10.1016/j.foreco.2007.08.030.

Shoo LP, Williams SE, Hero JM. 2005. Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology* **11**:1469–1476 DOI 10.1111/j.1365-2486.2005.00995.x.

Suorsa P, Huhta E, Nikula A, Nikinmaa M, Jäntti A, Helle H, Hakkarainen H. 2003. Forest management is associated with physiological stress in an old-growth forest passerine. *Proceedings of the Royal Society B: Biological Sciences* **270**:963–969 DOI 10.1098/rspb.2002.2326.

Thuiller W, Georges D, Engler R. 2015. biomod2. R package v. 3.1-64. *Available at https://cran.r-project.org/web/packages/biomod2/index.html*.

Thuiller W, Lafourcade B, Engler R, Araújo MB. 2009. BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography* **32**:369–373 DOI 10.1111/j.1600-0587.2008.05742.x.

Tôrres NM, De Marco P, Santos T, Silveira L, De Almeida Jácomo AT, Diniz-Filho JAF. 2012. Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. *Diversity and Distributions* **18**:615–627 DOI 10.1111/j.1472-4642.2012.00892.x.

Tsoar A, Allouche O, Steinitz O, Rotem D, Kadmon R. 2007. A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions* **13**:397–405 DOI 10.1111/j.1472-4642.2007.00346.x.

Turner MG, Gardner RH, O'Neill RV. 2001. *Landscape ecology in theory and practice. Pattern and process.* New York: Springer-Verlag New York, Inc.

Uuemaa E, Mander Ü, Marja R. 2013. Trends in the use of landscape spatial metrics as landscape indicators: a review. *Ecological Indicators* **28**:100–106 DOI 10.1016/j.ecolind.2012.07.018.

Uuemaa E, Roosaare J, Mander Ü. 2005. Scale dependence of landscape metrics and their indicatory value for nutrient and organic matter losses from catchments. *Ecological Indicators* **5**:350–369 DOI 10.1016/j.ecolind.2005.03.009.

VanDerWal J, Shoo LP, Johnson CN, Williams SE. 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist* **174**:282–291 DOI 10.1086/600087.

Villard M-A, Trzcinski MK, Merriam G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* **13**:774–783 DOI 10.1046/j.1523-1739.1999.98059.x.

Wang Y-H, Yang K-C, Bridgman CL, Lin L-K. 2008. Habitat suitability modelling to correlate gene flow with landscape connectivity. *Landscape Ecology* **23**:989–1000 DOI 10.1007/s10980-008-9262-3.

Wiens JA. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**:81–120 DOI 10.1146/annurev.es.07.110176.000501.

Wisz MS, Guisan A. 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecology* **9**:8 DOI 10.1186/1472-6785-9-8.

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, Elith J, Dudík M, Ferrier S, Huettmann F, Leathwick JR, Lehmann A, Lohmann L, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Phillips SJ, Richardson KS, Scachetti-Pereira R, Schapire RE, Soberón J, Williams SE, Zimmermann NE. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* **14**:763–773 DOI 10.1111/j.1472-4642.2008.00482.x.

Yackulic CB, Chandler R, Zipkin EF, Royle JA, Nichols JD, Grant EHC, Veran S. 2013. Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution* **4**:236–243 DOI 10.1111/2041-210x.12004.