# 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.

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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.

1 TITLE

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25  **ABSTRACT**

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27  abundance. High heterogeneity due to habitat alteration and fragmentation can influence the

28  realized niche of a species, lowering habitat suitability as well as reducing local abundance. We

29  investigate whether a relationship exists between habitat suitability and abundance and whether

30  both are affected by fragmentation. Our aim was to assess the predictive power of such a

31  relationship to derive advice for environmental management. As a model species we used a

32  forest specialist, the short-toed treecreeper (Family: Certhiidae; *Certhia brachydactyla* Brehm,

33  1820), and sampled it in central Italy. Species distribution was modelled as a function of forest

34  structure, productivity and fragmentation, while abundance was directly estimated in two central

35  Italian forest stands. Different algorithms were implemented to model species distribution,

36  employing 170 occurrence points provided mostly by the MITO2000 database: an artificial

37  neural network, classification tree analysis, flexible discriminant analysis, generalized boosting

38  models, generalized linear models, multivariate additive regression splines, maximum entropy

39  and random forests. Abundance was estimated also considering detectability, through N-mixture

40  models. Differences between forest stands in both abundance and habitat suitability were

41  assessed as well as the existence of a relationship. Simpler algorithms resulted in higher

42  goodness of fit than complex ones. Fragmentation was highly influential in determining potential

43  distribution. Local abundance and habitat suitability differed significantly between the two forest

44  stands, which were also significantly different in the degree of fragmentation. Regression

45  showed that suitability has a weak significant effect in explaining increasing value of abundance.

46    In particular, local abundances varied both at low and high suitability values. The study lends

47    support to the concept that the degree of fragmentation can contribute to alter not only the

48    suitability of an area for a species, but also its abundance. Even if the relationship between

49    suitability and abundance can be used as an early warning of habitat deterioration, its weak

50    predictive power needs further research. However, we define relationships between a species and

51    some landscape features (*i.e.* fragmentation, extensive rejuvenation of forests and tree

52    plantations) which could be easily controlled by appropriate forest management planning to

53    enhance environmental suitability, at least in an area possessing high conservation and

54    biodiversity values.

55

56    **INTRODUCTION**

57    In recent years considerable research effort has been involved in studying the influence of

58    landscape patterns on biodiversity, triggered by the wide availability of biological data, as well

59    as by the development of sophisticated species distribution models (SDMs), capable of

60    predicting the presence of a species as a function of environmental variables (Elith & Leathwick,

61    2009). The reliability of SDMs is based on the quality of occurrence data and the use of

62    environmental predictors linked to species occurrence (Austin, 2007). For instance, presence data

63    collected through nationwide standardised monitoring programmes provide enormous

64    advantages in using SDMs, due to the creation of large databases (Elith & Leathwick, 2009),

65    hosting large amounts of occurrences and covering a wide, biologically significant area.

66    Appropriate environmental predictors are those supposed to best describe the set of abiotic and

67    biotic conditions affecting species occurrence, *i.e.* those characterising the species ecological

68 niche (*sensu* Hutchinson; Hutchinson 1957; Holt 2009). Indeed, large-scale species distribution

69 modelling can be useful for addressing species-habitat relationships at multiple spatial scales in

70 order to understand the spatial variability in habitat selection (Farashi, Kaboli & Karami, 2013;

71 Chefaoui et al., 2015; Morand et al., 2015). Also, considering the spatial heterogeneity in the

72 environment has become essential in many studies regarding reproduction, meta-population

73 dynamics, gene flow, dispersal and connectivity (Bender, Tischendorf & Fahrig, 2003; Wang et

74 al., 2008; Ryberg et al., 2013). Recent studies have addressed this issue to propose alternative

75 conservation strategies (Nixon et al., 2014), to monitor landscape change (Darvishi, Fakheran &

76 Soffianian, 2015) and to give insight into the distribution of native and non-native species

77 (Kumar, Stohlgren & Chong, 2006). Moreover, spatial patterns are considered major drivers of

78 many ecosystem processes (Uuemaa, Mander & Marja, 2013).

79 Although landscape heterogeneity may promote biodiversity due to the increase in habitat types

80 (*i.e.* spatial heterogeneity) (Wiens, 1976; Loehle et al., 2005; Schindler et al., 2013), a highly

81 diverse landscape arising from anthropogenic fragmentation may result in the loss of natural

82 habitats and specialist species, which frequently require large patches of relatively unaltered

83 habitat (*e.g.* extensive areas of well-preserved forests) (Marvier, Kareiva & Neubert, 2004).

84 Therefore, fragmentation can sometimes produce a simplification of the biological community,

85 or biotic homogenisation across the landscape (McKinney & Lockwood, 1999). Such a

86 consequence derives from the loss of unique habitats, which are not replaceable in the short term

87 (Fahrig, 2003).

88 Species abundance is also influenced by spatial variability, being affected by spatial gradients in

89 the environmental parameters that form the environmental niche (Martínez-Meyer et al., 2013).

90 Optimal conditions can be found where the environmental parameters are close to the centroid of

91   the Hutchinsonian niche (Hutchinson, 1957). Hence, environmental variability can influence

92   both the presence and abundance of a species. Indeed, the decrease in abundance could warn

93   about a species decline in population and/or range extent earlier than a decrease in environmental

94   suitability. In fact, abundance could also be low in highly suitable regions, in response to local

95   limiting factors (VanDerWal et al., 2009).

96   The aim of our study was to investigate the relationship between environmental suitability and

97   abundance of a species, in response to fragmentation. However, true environmental suitability

98   can be expressed only by the whole set of environmental predictors and the local conditions that

99   can influence movements and interaction (Grinnell, 1917) and the persistence of those conditions

100  itself (Jackson & Overpeck, 2000). Such an approach may be unfeasible, as in our case.

101  Therefore we refer to a restricted set of factors influencing local or regional environmental

102  suitability, *i.e.* some environmental predictors, which are supposed to be related to the

103  probability of occurrence, and concern habitat suitability (HS) (Franklin, 2009). Among those

104  habitats that can be highly modified by human activities, our research focused on forests, where

105  unsustainable timber harvest can result in a patchy landscape and alter the habitat, adversely

106  affecting forest biodiversity (Donald et al., 1998; Penman, Mahony & Lemckert, 2005; Craig,

107  2007; Bearer et al., 2008; Shifley et al., 2008; Czeszczewik et al., 2014; Calladine et al., 2015;

108  Escobar et al., 2015). Woody plants are key elements in shaping the distribution of several bird

109  species *such as* birds (MacArthur, Recher & Cody, 1966; Cody, 1985). Landscape structures and

110  the spatial arrangement of habitat patches can affect both the abundance and distribution of birds,

111  acting as structural bio-modifiers (Uuemaa, Mander & Marja, 2013).

112  Therefore we selected as a model species a forest specialist bird, the short-toed treecreeper

113  (Family: Certhiidae; *Certhia brachydactyla* Brehm, 1820), and used landscape metrics as well as

114     forest variables to characterise the forest landscape and weight habitat suitability. The short-toed

115     treecreeper is considered a forest-dwelling passerine, and hence a forest specialist, being a

116     secondary cavity nester (Newton, 1994). It is usually found in oak or mixed-deciduous forests

117     (with prevalence of oak), where it nests inside small holes excavated by woodpeckers or left by

118     dead branches (Cramp, 1988). It is a resident species, with very limited movements, usually

119     restricted to post-juvenile dispersal (Cramp, 1988). Home range and territory size can also be

120     very limited, sometimes less than 1 ha (Cramp, 1988). The global range extends through most of

121     central/southern Europe, up to Turkey and the Caucasus, overlapping with *C. familiaris* in

122     central Europe (BirdLife International, 2012). Thus we assessed whether there was a relationship

123     between local abundance and HS. We hypothesise that the realized niche can be altered by

124     fragmentation, resulting in lower HS and abundance. If such a relationship emerges, we aim to

125     estimate its predictive power and usefulness in forest management and in conservation policies.

126     In addition, we modelled HS with several algorithms and compared results, to assess whether

127     different species distribution models (SDMs) follow the same pattern of response.

128     **METHODS**

129     One of the main advantages offered by SDMs relies on the use of occurrence data collected with

130     different methods (Tsoar et al., 2007). Therefore we used occurrence records from multiple

131     sources, that spanned from year 2000 to 2013. We relied mainly on the MITO2000 database

132     (*Monitoraggio ITaliano Ornitologico*, ITalian Ornithological Monitoring), an ongoing project

133     which started in 2000 and operates at a country-wide level (Fornasari et al., 2010). The project

134     uses point counts with unlimited radius (Blondel, Ferry & Frochot, 1981), sampling points being

135     randomly selected within a 1 km$^2$ grid square in the region of interest. Point counts were carried

136     out during a short time frame, from mid-May to mid-June. Occurrences of *C. brachydactyla*

137    were also extracted from the databases of the National Forest Service (Ufficio Territoriale della

138    Biodiversità, Castel di Sangro, AQ), and the LIFE+ ManFor C.BD project, which employed a

139    sampling design similar to MITO2000, albeit at a smaller spatial scale (~ 200 – 500 m). The

140    spatial coverage of the occurrences was limited to the administrative boundaries of the regions of

141    Lazio, Abruzzo and Molise, comprising 32,523 km², of which over one-third (12,309 km²) had

142    forest cover (fig. 1). The whole database was filtered from all the pseudo-replicated points that

143    fell into the same 1 km² grid. The database was further cleared of all the occurrences that were

144    located in unrealistic locations (*i.e.* non-forested areas), except for those < 300 m away from the

145    nearest forest patch, which were relocated to the nearest patch. Every occurrence was

146    georeferenced with GPS. Hence, for our purposes, the error in location was assumed to be the

147    same across the three datasets. The final database consisted of 170 occurrence points of *C.*

148    *brachydactyla* (tab. 1), of which 119 were supplied by the MITO2000 database, exceeding the

149    recommended minimum sample size (Wisz et al., 2008).

150    ***Species distribution models***

151    The SDMs were implemented using five environmental predictors, correlated with forest

152    structure, productivity and the degree of fragmentation, at a spatial resolution of 30 m. First, a

153    habitat type map, consisting of 12 classes, was created from the regional forest maps (Marchetti

154    et al. 2009; Garfì and Marchetti 2011; Anonymous 2012), aggregating all of the non-forest

155    habitat and distinguishing 11 forest types (tab. 1). Three landscape metrics were then calculated

156    from the habitat map, using FRAGSTATS v. 4 software (McGarigal, Cushman & Ene, 2012): 1)

157    *Diversity* (H'), a measure of patch type diversity within the landscape (Shannon & Wiener,

158    1949); 2) *edge density* (ED) which expresses the density (m ha⁻¹) of boundaries; 3) the

159    *aggregation index* (AI) which measures the degree of aggregation between forest patches (He,

160 DeZonia & Mladenoff, 2000). The first two metrics were implemented using a moving window

161 of 1000 m, as they can show little variability among different spatial scales and we were

162 interested in landscape features, avoiding the influence of small patches (Uuemaa, Roosaare &

163 Mander, 2005). By contrast, for AI a 300 m moving window was used, as we were interested, in

164 this case, in controlling how small patches aggregate across the landscape, according also to the

165 home range and territory size of the short-toed treecreeper (Cramp, 1988). Accordingly, we

166 chose to use the normalized difference vegetation index (NDVI) as a proxy of forest cover and

167 structure, integrating it into the modelling framework. The NDVI is highly correlated with the

168 leaf area index and the net primary productivity (Myneni et al., 1995; Pettorelli et al., 2005; Lee

169 et al., 2006) and was calculated from Landsat 8 multispectral images, with 30 m spatial

170 resolution. NDVI was computed over a mosaic of five images with cloud cover < 10%, collected

171 between July and August 2013, which had undergone the atmospheric correction procedure.

172 Finally, altitude was integrated through a digital elevation model (DEM) provided by the

173 National Institute for Environmental Protection and Research (ISPRA), available at

174 http://www.sinanet.isprambiente.it/it.

175 Spatial autocorrelations of the environmental predictors within occurrence points were tested

176 through a Mantel test in order to detect any spatial autocorrelations among occurrences (fig. S1).

177 Analyses were carried out with the R package '*ecospat*' (Broennimann, Di Cola & Guisan,

178 2016).

179 Among the eight selected algorithms, the maximum entropy (ME) used presence-only points in

180 combination with background samples, using only quadratic and hinge features to avoid

181 overfitting (Phillips, Anderson & Schapire, 2006; Elith et al., 2011). The other algorithms, which

182 were supplied with  pseudo-absences and true absences, were: an artificial neural network (ANN;

183    Segurado and Araujo 2004), classification tree analyses (CTA; Breiman et al. 1984; De'ath

184    2002), flexible discriminant analyses (FDA; Hastie et al. 1994), generalized boosting model

185    (GBM; Friedman 2001), generalized linear model (GLM; McCullagh and Nelder 1989),

186    multivariate additive regression spline (MARS; Moisen and Frescino 2002) and random forest

187    (RF; Breiman 2001) (tab. 2). Ten thousand absence points were sampled in the environmental

188    background (Elith et al., 2006), comprising 975 points of actual absence derived from the

189    MITO2000 database and 9025 pseudo-absences, randomly selected within the area where the

190    logistic output of ME was less than 0.2 (Chefaoui & Lobo, 2008; Wisz & Guisan, 2009),

191    representing an adequate number of pseudo-absences (Barbet-Massin et al., 2012). SDMs were

192    trained using 70% of randomly selected occurrences, while the remaining 30% were used for

193    testing; the procedure was iterated 30 times (except for ME with 50 iterations) (further details are

194    provided in table 2). The area under the curve (AUC) of the receiving operating characteristic

195    (Hanley & McNeil, 1982) was used to evaluate the predictive power of the SDMs. To improve

196    the readability of SDM outputs, sensitivity (*i.e.* the proportions of correct positive prediction)

197    and specificity (*i.e.* the proportion of correct negative prediction) and the true skill statistic (TSS)

198    were also reported (Allouche, Tsoar & Kadmon, 2006; Lobo, Jiménez-Valverde & Real, 2008).

199    The importance of each environmental predictor was calculated following Thuiller et al. (2009).

200    Analyses were carried out with the software MaxEnt (Phillips, Anderson & Schapire, 2006) and

201    the *biomod2* package integrated in R (Thuiller et al., 2009; R Core Team, 2015; Thuiller,

202    Georges & Engler, 2015).

203    ***Abundance estimation***

204    Abundance was estimated in two forest stands used as test sites of the LIFE+ ManFor C.BD:

205    Bosco Pennataro Regional Forest and Chiarano-Sparvera Regional Forest. Bosco Pennataro (BP,

206    41° 44' N, 14° 11' E, 1000 m a.s.l.) consists of a multi-layered high forest stand dominated by

207    turkey oak (*Quercus cerris*). Chiarano-Sparvera (CS, 41° 51' N, 13° 57' E, 1700 m a.s.l.) is a

208    pure beech (*Fagus sylvatica*) forest, in transition from coppice to high forest. Following a

209    systematic design, 27 and 23 sampling points, 125.5 m (± 19.7 sd) away from one another, were

210    selected in BP and CS, respectively. Surveys were carried out from May to June (2012 in CS;

211    2013 in BP) from sunrise till 11:00 a.m. At every point, each individual detected by aural/visual

212    cues during a five-minute count was recorded. Each point was visited two to six times (average =

213    3.4; total = 177).

214    Local abundance was estimated with N-mixture models (Royle, 2004b). This approach considers

215    local abundance (*i.e.* abundance estimated in each sampling point) as an independent random

216    point process (Royle, 2004a). Two separate models were built for BP and CS, respectively: with

217    and without detectability variation among occasions. Model fit and overdispersion (also called c-

218    hat) was  tested through a Pearson $\chi^2$ goodness-of-fit test, with 1000 bootstrap resampling

219    (MacKenzie & Bailey, 2004). Model selection proceeded through Akaike's Information

220    Criterion, which assigns scores both to the likelihood of the model and the number of parameters

221    included (Burnham & Anderson, 2002). Spatial dependence of estimates was assessed with the

222    Moran test and index calculation (Moran, 1950). Analyses were carried out using the packages

223    *unmarked* (Fiske & Chandler, 2011), *AICmodavg* (Mazerolle, 2015) and *spdep* (Bivand & Piras,

224    2015) implemented in R (R Core Team, 2015).

225    ***Statistical analyses***

226    Local abundances (*i.e.* the abundance at every sampling point) in BP and CS were tested for

227    differences with an *F*-test, followed by a *t*-test. Habitat suitability values, defined as the SDM

228    outputs, were then extracted from a discrete area surrounding every abundance point. Width of

229   the area in question was proportional to local abundance and was derived by transforming the

230   estimated population size (*i.e.* the sum of local abundances) into densities (ind./ha): the area of

231   interest for density transformation was given by the minimum convex polygon among the

232   sampling points. The difference between BP and CS environmental suitability values was tested

233   by an *F*-test and a *t*-test. The landscape metric values were also tested for difference with the

234   same methods.

235   The relationship between abundance and environmental suitability can form a triangular

236   envelope, where increasing values of environmental suitability are matched by increasing values

237   of the maximum abundance, not just the mean abundance (VanDerWal et al., 2009). Therefore,

238   quantile regression can best provide the opportunity to explore the relation between

239   environmental suitability and the upper quantiles of the abundance (Cade, Noon & Flather,

240   2005). The triangular envelope can predict maximum abundance, given a suitability value, due to

241   the increase in the slope of regressions of upper quantiles, while intercepts remain similar

242   (VanDerWal et al., 2009). However, two factors can mask the results: first, random variation at

243   every point also due to local limiting factors that are not feasible to model; secondly, the spatial

244   structure of the data, that can generate autocorrelation. Therefore, quantile mixed regressions

245   were implemented to model the abundance as a function of HS values of every SDM, with a null

246   random term and a grouping factor identifying the two locations. The random effect is estimated

247   through best linear prediction (Geraci & Bottai, 2013). Model fit was assessed for every quantile

248   through comparison of AIC scores with the null model of the corresponding quantile (Burnham

249   & Anderson, 2002). Statistical analysis was carried out with the *lqmm* package (Geraci, 2014) in

250   R (R Core Team, 2015).

251   **RESULTS**

252    Each SDM showed an AUC > 0.9, except for FDA (tab. 2). Among them, RF ranked the highest

253    value (AUC = 1). However, the geographical projections of the SDMs proved dissimilar (see

254    supplementary materials, fig. S2). The importance of each environmental predictor had the same

255    pattern for every algorithm, with forest type and NDVI proving the most important (fig. 2). The

256    importance of the three landscape metrics (H, AI, ED) indicates that the spatial configuration of

257    landscape structures exerts a major influence on potential distribution.

258    Abundance models that performed best in both study areas were those in which detectability was

259    invariant between sessions. Detectability was 0.34 (± 0.11 SE) in Bosco Pennataro and 0.21 (±

260    0.27 SE) in Chiarano Sparvera. Local abundances significantly differed between the two areas ($F$

261    = 0.77, p = 0.53; $t$ = -3.57, p < 0.001), and mean estimates were 1.54 (± 0.52 SE) in BP and 0.86

262    (± 1 SE) individuals/point in CS. Both models returned a good fit, with no overdispersion (BP: $\chi^2$

263    = 64.3, p = 0.997, c-hat = 0.687; CS: $\chi^2$ = 52.5, p = 0.391, c-hat = 1). Estimates did not show

264    spatial autocorrelation in the two forest stands, obtaining a Moran I of 0.11 (p = 0.14) and -0.26

265    (p = 0.92) for BP and CS, respectively.

266    Habitat suitability also proved different between BP and CS, for every SDM (tab. 3), and HS was

267    higher in BP. In parallel, the values of landscape metrics significantly differed between the two

268    forest stands except for edge density (tab. 3). Specifically, Bosco Pennataro landscape structure

269    resulted in larger and less scattered patches (AI = 98), equally distributed among types (H' =

270    0.93), compared to CS (AI = 92.6; H' = 0.76). Hence, landscape metrics showed a more

271    fragmented landscape in CS than in BP, as expected.

272    Quantile regression showed a positive relationship between abundance and HS (fig. 3 and fig.

273    S3). No differences emerged for the regression slope of each quantile, while intercept values

274    proved more variable. Moreover, the majority of slopes were not significant except for CTA,

275    GBM and GLM (see supplementary materials, tab. S1), even if AIC comparison indicated that

276    most of the quantiles performed better than the corresponding null model (tab. 4).

277    **DISCUSSION**

278    We examined the abundance and habitat suitability resulting from many algorithms for species

279    distribution modelling (Elith et al., 2006; Li & Wang, 2013) of a forest-dwelling passerine in a

280    region with different degrees of fragmentation. Although SDMs showed high AUCs,

281    geographical projections varied quite substantially among algorithms, even if their explanatory

282    variables followed the same pattern of importance scoring. Moreover, AUC computation for ME

283    differs from the other algorithms, which made use of (pseudo) absences, being not comparable

284    (Yackulic et al., 2013). Several studies that compared SDM outputs differed substantially

285    (Segurado & Araujo, 2004; Elith et al., 2006; Moisen et al., 2006; Meynard & Quinn, 2007).

286    Among those that based their comparison on AUC, ANN was favoured over CTA and GLM

287    (Segurado & Araujo, 2004) and GBM and ME were favoured over MARS and GLM (Elith et al.,

288    2006). GBM and GLM were preferred to CTA also by other authors (Moisen et al., 2006;

289    Meynard & Quinn, 2007). What emerged from the literature is that complex models usually

290    outperform simple models, especially when they involve specialist species (Jiménez-Valverde,

291    Lobo & Hortal, 2008; Li & Wang, 2013). Indeed, our results are not totally concordant with

292    findings elsewhere, simple models like GLM and GBM having scored higher AUC values.

293    However, the use of AUC has been criticised by many authors even if there are currently no

294    consensus methods to assess the predictability of SDMs (Austin, 2007; Lobo, Jiménez-Valverde

295    & Real, 2008). Specifically, the AUC does not consider the goodness of fit of a model and it is

296    higher when more pseudo-absences in unsuitable localities are included in the model (Lobo,

297    Jiménez-Valverde & Real, 2008). Nevertheless, its use is still widespread (Elith & Graham,

298   2009; Barbet-Massin et al., 2012). It should also be pointed out that, even if we used a large

299   number of (pseudo) absences, we also employed a larger number of presence points than what is

300   usually found in the literature (e.g. Pearson et al., 2007).

301   SDM output can usually be considered as a probability of occurrence, somewhat related to

302   habitat suitability (Franklin, 2009). In the case of ME, this is achieved after logistic

303   transformation (Phillips & Dudík, 2008). This approach has been criticised because of the

304   frequent violation of two major assumptions: randomness of the samples and constant

305   detectability among individuals (Royle et al., 2012; Merow, Smith & Silander, 2013). Indeed, the

306   logistic output uses a rather subjective intercept of 0.5, which is valid, though its reliability is not

307   proven (Royle et al., 2012). Use of pseudo-absence also needs caution, since the background in

308   which sampling takes place has both suitable and unsuitable locations (Pearce & Boyce, 2006).

309   However, we employed an analytical framework designed to reduce this source of bias. The

310   randomness of the presence points is due to the use of occurrences coming from a standardised

311   monitoring programme. For the same reasons, we assume that the variability in detectability is

312   reduced to the minimum, demonstrating this issue also in the two forests where we estimated

313   abundance (*i.e.* BP and CS). Finally, our use of the logistic output of ME, as well as of its

314   subjective intercept of 0.5, is based upon the consideration that 37% of the study area is covered

315   in forest. Therefore, assuming an intercept of 0.5 does not seem too far from reality scenario.

316   Indeed, ME has been proved to be one of the most reliable SDMs when only presence data are

317   available (Franklin, 2009; Merow, Smith & Silander, 2013). Our use of ME, moreover, was

318   functional to the selection of pseudo-absences, which were not selected within the entire region,

319   but only in a restricted area considered unsuitable by ME. As a consequence, we also assume that

320   our method of selecting pseudo-absence greatly reduced an eventual bias. At the very end, we

321 considered SDM outputs as a habitat suitability index, which we could assume to be related to

322 actual environmental suitability (VanDerWal et al., 2009; Brambilla & Ficetola, 2012).

323 For reliable modelling, it is necessary to use ecologically relevant environmental predictors

324 (Austin, 2007), even if it is not possible to include every environmental variable thought to affect

325 the distribution of a species (Elith & Leathwick, 2009). We based the choice of environmental

326 variables on both the known species-habitat relationships and on the possibility of obtaining

327 relevant information to steer management, relying on forest type, structure, productivity and

328 fragmentation. Forest type and NDVI proved the most important variables in predicting the

329 distribution of the short-toed treecreeper. The NDVI is not only positively correlated to net

330 primary productivity (Myneni et al., 1995; Pettorelli et al., 2005), but also to the structural

331 complexity of forests (Manes et al., 2010). As a consequence, among the same forest type, a

332 higher NDVI is related, given that all other variables are comparable, to more structured, multi-

333 layered forests or to forest patches that are more productive or that have a higher leaf area index,

334 where specialist birds can find a more suitable habitat (Newton, 1994; Carrillo-Rubio et al.,

335 2014). Obviously, this conclusion also depends on the patch size and the degree of

336 fragmentation, which are intertwined with NDVI and forest type. Indeed, a substantial influence

337 of landscape structure in defining habitat suitability was clearly apparent when taking into

338 account the three metrics together. Responses to fragmentation are species-specific and, usually,

339 the more specialist a species, the more negative its response (Devictor, Julliard & Jiguet, 2008;

340 Rueda et al., 2013). SDM outputs showed higher HS in localities in less fragmented landscapes,

341 in agreement with the literature on forest specialist birds (Fahrig, 2003).

342 We used hierarchical statistical analysis of abundance to obtain unbiased estimates, corrected for

343 detectability (Royle, 2004a). The significant difference in abundances between Bosco Pennataro

344 and Chiarano-Sparvera is matched by the difference in the suitability of the two forests.

345 Therefore, differences in abundance, HS and landscape metrics matched the same pattern: in

346 locations with more degraded forest, both HS and abundance scored lower values, even though

347 abundance showed higher variability, confounding the hypothesised relationships with HS.

348 Our results suggest that there is a positive relationship between habitat suitability and treecreeper

349 abundance, even if the hypothesised triangular envelope (VanDerWal et al., 2009) did not

350 emerge. However, its predictive power was quite weak, due to high abundance variability in both

351 low and high HS locations. Extensive research has yielded little evidence for the relationship

352 between demographic parameters and HS (Pearce & Ferrier, 2001; Nielsen et al., 2005; Jiménez-

353 Valverde et al., 2009). Related findings are often discordant (Jiménez-Valverde et al., 2009;

354 Tôrres et al., 2012) and many concerns are raised on the controversial and often unconfirmed

355 empirical relationships between ecological processes and landscape patterns (Turner, Gardner &

356 O'Neill, 2001; Kupfer, 2012). That said, the relationship can be masked by the many unmodelled

357 environmental variables that can conceal local suitability (Lobo, Jiménez-Valverde & Real,

358 2008). For this reason, VanDerWal et al. (2009) concluded that just the upper limit of

359 abundance, and not its mean value, is predictable from HS. However, this relationship has been

360 widely found to be very weak due to the difficulty to obtain reliable estimates of both abundance

361 and HS (Jiménez-Valverde, 2011; Oliver et al., 2012; Tôrres et al., 2012). Some exceptions are

362 presumably due to the use of indexes of abundance, instead of actual estimates (de Moraes

363 Weber & Viveiros Grelle, 2012; Gutiérrez et al., 2013). Indeed, our approach was based not only

364 on abundance estimates but also on HS values from different algorithms and averaged over the

365 likely home range size. Moreover, our use of landscape features as predictive variables could

366     have enhanced model performance since other studies (*e.g.* Tôrres et al., 2012), based mostly on

367     climatic variables, found positive but weaker relationships between HS and abundance.

368     This result, though confirming the existence of a relationship, also highlights the limits of the

369     SDM approach, suggesting that low HS can also occur in areas of high abundance, probably due

370     to environmental factors that are not considered in modelling which may increase the actual HS

371     of the area.

372     **CONCLUSION**

373     Birds are considered good biodiversity indicators, especially to monitor habitat alteration (*e.g.*

374     fragmentation) (Gregory et al., 2008; Carrillo-Rubio et al., 2014; Czeszczewik et al., 2014). For

375     instance, in the context of biotic homogenization, one likely effect is the disappearance of

376     specialist species which are more closely associated to unaltered forests (McKinney &

377     Lockwood, 1999). Negative effects of habitat alteration can persist over years (Kendrick et al.,

378     2014). Thus identification of the main species-habitat relationships is important to prevent the

379     disappearance of more susceptible species (Villard, Trzcinski & Merriam, 1999; King &

380     DeGraaf, 2000). Further, fragmentation can cause the disappearance of the specialist component

381     of biodiversity (Fahrig, 2003). Such processes can alter biological, ecological and demographic

382     traits like brood survival and growth (Suorsa et al., 2003; Le Tortorec et al., 2012), occupancy or

383     population size (Schmiegelow, Machtans & Hannon, 1997; Villard, Trzcinski & Merriam, 1999;

384     Cooper & Walters, 2002). Through SDMs, such results can be transposed into geographic

385     projection and inform conservationists and practitioners (Ferrier et al., 2007; Maiorano et al.,

386     2015). Therefore, modelling how fragmentation can affect the distribution of a species and

387     understand the eventual relations with population decrease, can greatly improve conservation and

388     management plans.

389    A forest landscape is, in most European cases, a human-modified landscape whose properties,

390    like patch size, can affect many species (Gil-Tena, Torras & Saura, 2008). Our approach takes

391    into account such issues in order to provide information-based advice. In this way, we define the

392    relationships between a species and some "directly adjustable" landscape features. The Chiarano-

393    Sparvera forest stand is naturally located in a more fragmented landscape than is Bosco

394    Pennataro. Hence, the abundance response (*i.e.* decrease) of the short-toed treecreeper is matched

395    by habitat choice. Fragmentation, extensive rejuvenation of forest stands and tree plantations are

396    all factors that can contribute to alter the suitability of an area. Since habitat alteration can

397    decrease species abundance sooner than effectively reducing their geographic range (Shoo,

398    Williams & Hero, 2005), identification of areas of low HS, where impact on abundance is more

399    likely to cause local extinctions, could act as an early warning for species conservation. In our

400    approach, these threats can occur on a large scale, can be related to possible changes in

401    abundance and then used to inform practitioners and managers. Moreover, prediction of future

402    land use scenarios can be implemented.

403    However, our results are a case study, limited to a single specialist species, strictly linked to

404    mature well-preserved forests. This approach could be extended over different kinds of habitats

405    and species, other than forests. Moreover, the modelling should be refined to include other

406    potential resources and limiting factors, whether biotic or abiotic, in order to obtain more robust

407    HS prediction (Guisan & Thuiller, 2005). The magnitude of the relationship between HS and

408    abundance can then be used as a form of model validation (Lobo, Jiménez-Valverde & Real,

409    2008), thus helping to steer sound land use management and conservation planning.

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745

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 (km$^2$) | 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 |

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 | 10000 | 5-fold cross validation | 0.949 | 92.045 | 89.689 | 0.771 |
| classification tree analyses | CTA | 10000 | 5-fold cross validation | 0.918 | 85.795 | 93.839 | 0.792 |
| flexible discriminant analyses | FDA | 10000 | Default with MARS to increase predictive power | 0.894 | 82.955 | 93.849 | 0.768 |
| generalized boosting model | GBM | 10000 | 5000 maximum trees, 5 interaction and 10-fold cross validation | 0.961 | 93.75 | 94.529 | 0.842 |
| generalized linear model | GLM | 10000 | AIC-based stepwise model selection | 0.959 | 93.182 | 91.159 | 0.835 |
| multivariate additive regression splines | MARS | 10000 | Spline knots are determined automatically | 0.913 | 89.205 | 89.129 | 0.782 |
| maximum entropy | ME | No; 10000 background points | 1000 bootstrap iterations | 0.929 | - | - | - |
| random forest | RF | 10000 | 750 trees, 10-fold cross validation | 1 | 100 | 99.98 | 1 |

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

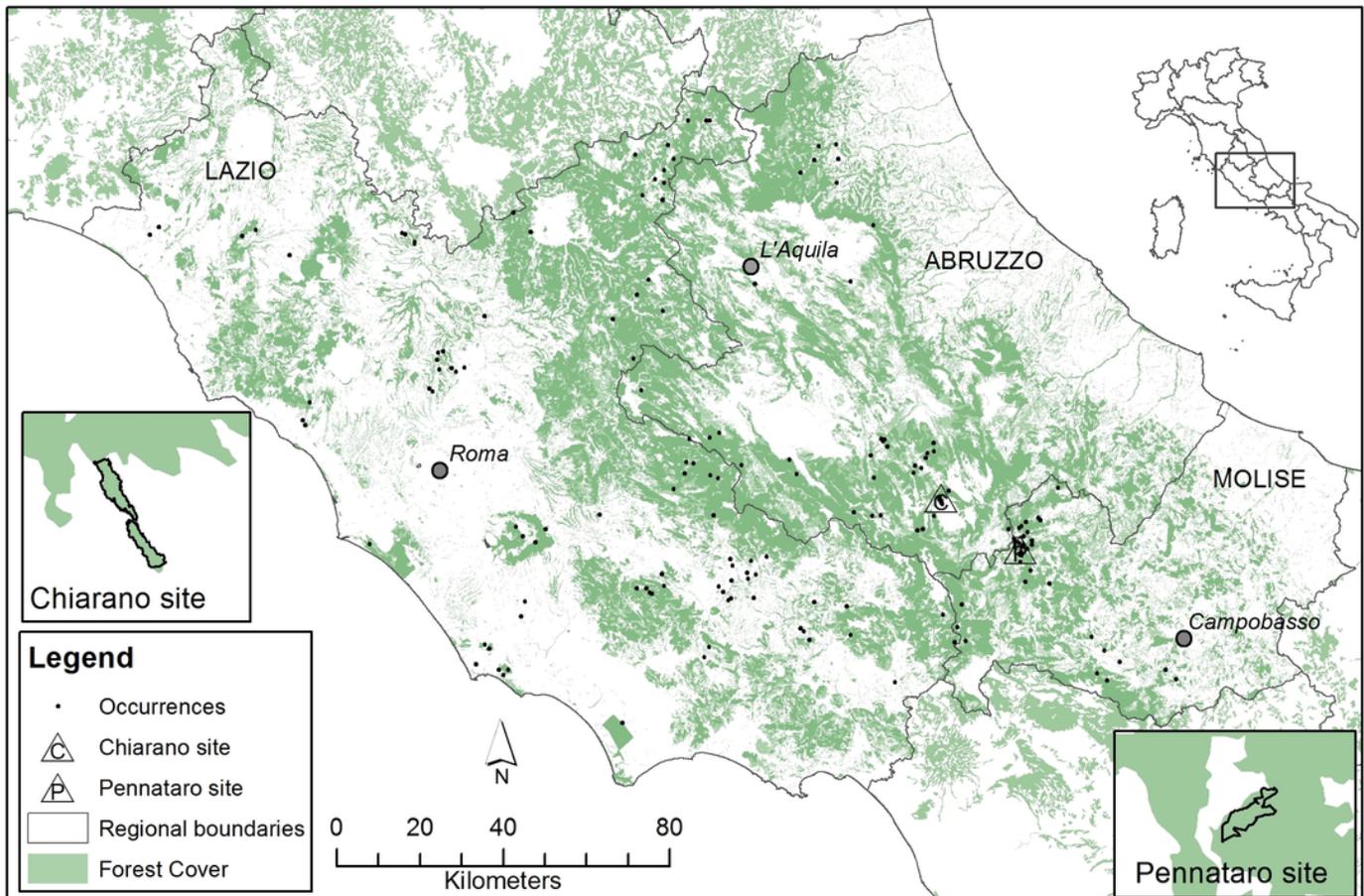
H' = Shannon index of patch type diversity; Ed = edge density; Ai = aggregation index; $F$ = Fisher's test; $t$ = t test; P = p value; model abbreviation are given in table 2

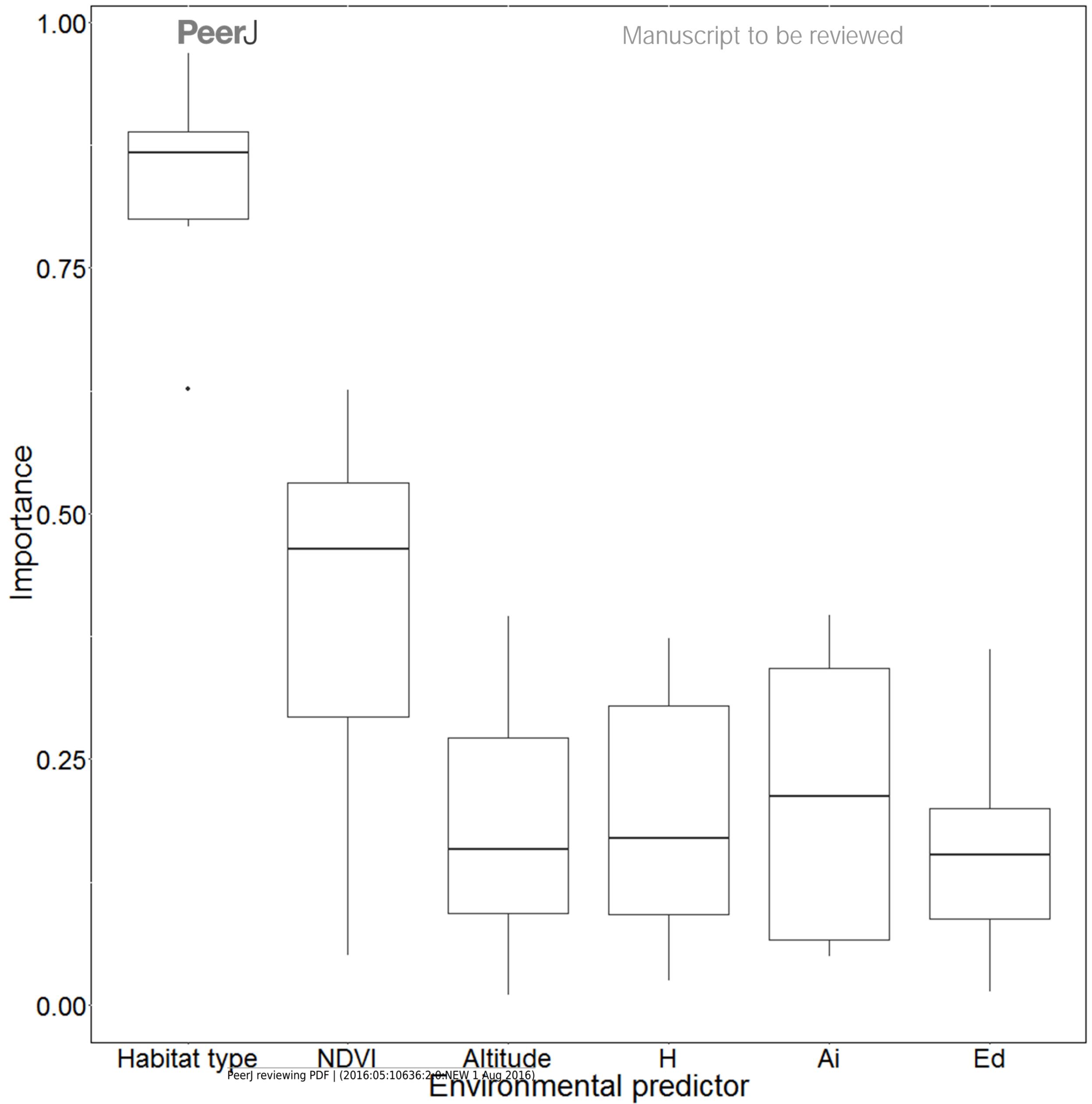
|  | *F* | P | *t* | p |
|---|---|---|---|---|
| **Metric** | | | | |
| H' | 0.065 | 0.000 | 3.3342 | 0.0027 |
| Ed | 0.3583 | 0.0134 | -1.5038 | 0.1392 |
| Ai | 0.221 | 0.000 | 7.1504 | 0.000 |
| **Model** | | | | |
| ANN | 0.07 | 0.000 | -36 | 0.000 |
| CTA | 4.901 | 0.000 | -9.93 | 0.000 |
| FDA | 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 |

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 |

# 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.

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.

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.