

1 ORIGINAL ARTICLE

2 **How do the species' ecological and biological traits affect the application of**  
3 **the Island Biogeography Theory in fragmented landscapes?**

4

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22 **ABSTRACT**

23 **Aim.** Overall species richness in habitat remnants is seldom explained by the Island Biogeography  
24 Theory (IBT). Herein, we investigated how ecological and biological traits determine different species  
25 responses to the IBT laws. In particular, we tested the effectiveness of the IBT in explaining the species  
26 richness of three ecological groups: *generalist*, *edge* and *interior* species (community-level analysis).  
27 We also investigated the species-specific responses to fragment covariates (species-level analysis). This  
28 has a great importance for conservation purposes, as it allows the identification of species, or group  
29 of species, that could serve as indicators of different fragmentation degrees.

30 **Location.** Broadleaved forests in western Lombardy (northern Italy)

31 **Methods.** We evaluated bird species richness in 344 forest fragments. Fragment Area (FA), Distance  
32 from the nearest Source Area (>1000 ha) (DSA) and Number of neighbouring Fragments (NF) were  
33 calculated for each fragment. Using Poisson GLMs, we assessed the effect of fragment covariates at  
34 the community level. We also investigated the association between each species and particular  
35 fragmentation conditions by using the Indicator Species Analysis.

36 **Results.** The overall *forest-dependent* species richness was affected only by DSA (negatively) and NF  
37 (positively), while *generalist* and *interior* species richness also showed a significant relationship with  
38 FA (positive). Conversely, *edge* species richness increased with FA, but also with the DSA. The Indicator  
39 Species Analysis identified eight species, gathered in four groups strongly associated with specific  
40 fragmentation contexts.

41 **Main conclusions.** The results showed the strong influence of ecological and biological traits on  
42 species distribution in fragmented landscapes. *Interior* species richness responded better than that of  
43 other ecological groups to the IBT laws, making it the best candidate to play the role of proxy of  
44 fragmentation effects. However, not all *interior* species showed the same sensitivity to fragment size  
45 and isolation.

46

47 **INTRODUCTION**

48 Forest fragmentation is recognized as one of the major threats to global biodiversity as it is the human-  
49 induced phenomenon with the strongest effect on animal species distribution (Debinski & Holt, 2000;  
50 Fischer & Lindenmayer, 2007). Two theories describe the mechanism of this process: the Island  
51 Biogeography Theory (IBT; MacArthur & Wilson, 1967) and the Metapopulations Theory (Levins, 1969).  
52 The first one describes the effects of habitat fragment size and isolation on species richness (Debinski  
53 & Holt, 2000): the smaller and more isolated fragments are, the fewer are the species expected to  
54 occur within them (Diamond, 1975; Wilson & Willis 1975; Terborgh, 1976). The second one describes  
55 the spatial arrangement and dynamics of subpopulations in fragmented landscapes (Arnold et al.,  
56 1993; McCullough, 1997). Several studies combined these two theories in order to explain species  
57 richness as the balance between extinction and colonization in fragmented terrestrial contexts.  
58 According to the IBT and metapopulation theory, these processes depend on spatial covariates the  
59 physical characteristics of residual habitat fragments, such as their size and distance from source areas  
60 (e.g. large blocks of habitat), and the surrounding landscape context (e.g. the number of neighbouring  
61 habitat fragments) (Collinge, 1995; Laurence & Bierregaard, 1996; Lindenmayer et al., 2002; Watson  
62 et al., 2004). However, in some cases, the results of these studies were different from those expected  
63 (Margules, 1996; Schemiegelow et al., 1997; Davies & Margules, 1998; Margules et al., 1998). In fact,  
64 colonization and extinction processes also depend on species-specific life-history traits, such as  
65 ecological and biological traits (Öckinger et al., 2010; Franzén et al., 2012). In particular, in terrestrial  
66 contexts the relationships between species richness and fragment area and isolation, as postulated by  
67 the IBT, are often masked by the lack of an abrupt contrast between suitable and unsuitable habitats  
68 (as in the case of an island surrounded by the ocean), and by the absence of a highly impermeable  
69 matrix (as the ocean is for terrestrial island species). Indeed, in these contexts, species richness in  
70 habitat fragments is determined by the presence of species with different ecological traits, such as  
71 species intimately linked to habitat remnants (interior species), species linked to habitat remnants, but

72 not so negatively affected by the adjacent matrix (generalist species), or species that require the  
73 presence of transitional habitats (edge species). The IBT was actually developed for oceanic islands,  
74 where communities are typically closed or unitary (*sensu* Clements, 1916), and may be viewed as units  
75 operating mainly within themselves, while in terrestrial contexts communities are typically open (*sensu*  
76 Gleason, 1926). In addition, in terrestrial landscapes, results different from those postulated by the IBT  
77 can occur because species-specific biological traits (e.g. dispersal capability and reproductive potential)  
78 lead to a strong differentiation in species immigration and extinction rates, as a consequence of the  
79 high variability of both remnants quality and matrix permeability. Thus, the combination of species-  
80 specific ecological and biological traits determine a high heterogeneity in species responses to  
81 fragmentation. On the one hand, the preference of some species for small fragments can mask the  
82 species-area relationship as postulated by the IBT. In particular, a higher species richness in small  
83 fragments, where the ratio of edge and core area is maximized, could be due to a high number of edge  
84 species (Paton, 1994) or to the prevalence of generalist species in the overall species richness (Gascon  
85 & Lovejoy, 1998). On the other hand, the negative effect of isolation on species richness could be  
86 masked by the species' biological traits (Watson et al., 2004). For instance, some species are not  
87 affected by isolation because they are highly mobile (Margules et al., 1982; Ambuel & Temple, 1983)  
88 or because they are not so negatively affected by the matrices surrounding their habitat patches  
89 (Andrianarimisa et al., 2000; Renjifo, 2001). Despite all these caveats are widely known, there are still  
90 few empirical studies explicitly addressing how ecological and biological traits affect the relationship  
91 between species distribution and spatial covariates in fragmented landscapes (Henle et al. 2004).  
92 Clearly, this has a great importance from the conservation point of view when the intent is to use  
93 species, or groups of species, as surrogates of fragmentation degree.

94 This research was aimed at investigating how the ecological and biological traits of species could affect  
95 the application of the IBT on bird communities in fragmented broad-leaved forests within a wide area  
96 in northern Italy. First of all, we evaluated the robustness of the application of the IBT laws on the  
97 richness of overall *forest-dependent* species (i.e. excluding all matrix species). Subsequently, we split

98 the whole set of species into the following three groups, based on ecological traits, *generalist*, *edge*  
99 and *interior* species. We then tested how effective the IBT was in explaining species richness  
100 (community-level analysis). Finally, we applied the IBT at the single species level. In particular, we  
101 investigated the association of each species with specific combinations of IBT spatial covariates. This  
102 allowed us to assess how the distribution of each species was affected by fragments size, distance from  
103 source areas and number of surrounding patches, according to its specific ecological and biological  
104 traits (species-level analysis).

105 The community-level analysis led to the identification of the ecological groups that better responded  
106 to the IBT laws and, thus, were more sensitive to forest fragmentation. In other words, we were able  
107 to identify the ecological groups that could be used as indicators of landscape fragmentation. The  
108 species richness of ecological groups, however, might not always be the most valuable proxy of  
109 fragmentation, because it does not take into account species-specific biological traits. On the other  
110 hand, the species-level analysis, which accounts for species life-history traits, allowed us to identify  
111 species, or groups of species, which could serve as indicators of specific fragmentation contexts.

112

## 113 **MATERIALS AND METHODS**

### 114 **Study area**

115 The study was carried out in the western part of Lombardy (northern Italy), in an area of about 9,000  
116 km<sup>2</sup> where forests cover 23% of the total surface. The study area can be divided into three main sub-  
117 regions: the Prealps in the North; the lowland (below 300 m a.s.l.) in the central part; and the  
118 Apennines in the South (Figure 1). The Prealps and the Apennines are characterized by a mainly  
119 continuous forest cover. The lowland is crossed from North to South by the Ticino Natural Park, a 220  
120 km<sup>2</sup> wide protected area, with residual continuous forests following the course of the Ticino River. The  
121 remaining part of the lowland area has been highly modified, with intensive corn crops prevailing in  
122 the central and eastern part, and rice paddies in the West (Bani et al., 2006). Small, residual

123 broadleaved forest fragments (95% of which are smaller than 10 hectares) are scattered in the lowland  
124 cultivated area.

#### 125 **Bird data**

126 Bird data were obtained from a long-term monitoring program of breeding birds in Lombardy (Bani et  
127 al., 2009). This type of large-scale projects has the advantage of providing a large amount of data  
128 collected over wide areas. However, they usually do not consider the collection of data by means of  
129 multiple surveys in the same season, thus making it impossible to account for species detection  
130 probability. In particular, the Lombardy breeding bird monitoring program does not even rely on fixed  
131 sites, since the sampling units are randomly extracted each year.

132 The variability of species-specific detection probability is a potential problem in studies aimed at  
133 estimating species richness. Therefore, the use of multi-species data requires the assumptions that  
134 detection probability does not have a strong effect on inferences (Morelli, 2015). In our opinion, the  
135 large dataset used for this research may limit this potential bias, at least by reducing the noise  
136 produced by stochasticity in the detection of the rarest species.

137 Data were collected using a standardized method, based on the unlimited distance point count  
138 technique (Blondel et al., 1981; Fornasari et al., 1998), with a minimum distance of at least 500 m  
139 between sampling locations. In order to limit the effects of the within-species detection probability,  
140 bird surveys were performed each year during the breeding season (10<sup>th</sup> May – 20<sup>th</sup> June), from sunrise  
141 to 11.00 a.m., only in good weather conditions (sunny to cloudy, without rain or strong winds). The  
142 point count technique allows detecting bird species pertaining to *Columbiformes*, *Cuculiformes*,  
143 *Apodiformes*, *Coraciiformes*, *Piciformes*, *Passeriformes*, as well as common raptors (Bani et al., 2009).

144 For this research, we selected all the point counts performed in forest patches or within a 250 m buffer  
145 around them. We chose this distance, because it could be considered the maximum detection distance  
146 for most of the bird species surveyed. We only selected point counts performed from 2007 to 2014,

147 since no significant changes in broadleaved forest cover (less than 0.3%) occurred during that period  
148 in the study area. This was verified by comparing the available DUSAF 1:10,000 digital maps  
149 (Destinazione d'Uso dei Suoli Agricoli e Forestali [Classification of Agricultural and Forest Lands]):  
150 DUSAF 2.1 (ERSAF, 2007) and DUSAF 4 (ERSAF, 2014). In order to evaluate the effect of forest  
151 fragmentation, we only considered *forest dependent* species, defined as those species breeding in  
152 forest habitats. Subsequently, we divided the whole set of *forest-dependent* species into three  
153 ecological groups, based on literature information (Cramp & Simmons, 2006): *generalist* (forest-  
154 dependent species inhabiting either edge or interior habitats), *edge* and *interior* species.

### 155 **Landscape data**

156 As land-use cartography we used the most recent digital map available for the study area (DUSAF 4;  
157 ERSAF 2014). In particular, we took into account all patches belonging to one of the following  
158 categories of forest cover: broadleaved forests (DUSAF class: 311), mixed forests (DUSAF class: 313)  
159 and broadleaved reforestations (DUSAF class: 314). Using Arcgis 10 (ESRI, 2011), we merged all  
160 fragments that were less than 25 m apart. We chose this threshold, as it represents the width of a  
161 typical secondary road, the digitalization of which often leads to a subdivision of a single forest patch  
162 (as should be perceived by birds) in different forest polygons. In order to avoid the sample size effect  
163 for large fragments (larger than 100 ha), which could affect the characterization of bird communities,  
164 we only selected forest patches with a point counts density higher than 1 points/100 ha. On the whole,  
165 we considered a total of 366 patches. As we were interested in ascertaining the effects of forest  
166 fragmentation, we also excluded all patches larger than 1000 ha, which could be considered as source  
167 areas (Watson et al., 2004). In those large patches, the percentage of *forest-dependent* species  
168 detected ranged from 61% (for the smaller patch, just over 1000 ha) to 96% (for the larger patch, about  
169 575,000 ha) of the whole pool of *forest-dependent* species. For each of the 344 remaining forest  
170 fragments, we calculated the following three spatial variables: Fragment Area (FA), minimum Distance  
171 from the nearest Source Area (DSA), and Number of neighbouring Fragments in a buffer of 1000 m

172 (NF). We considered the latter variable in order to account for the possible “internal colonization”  
173 played by immigrants within the archipelago (Simberloff & Abele, 1982; Gotelli, 2008).

#### 174 **Community-level analysis**

175 In order to test the effectiveness of IBT in explaining bird species richness in fragments, we performed  
176 Generalized Linear Models (GLMs) using a Poisson distribution. Model covariates were the logarithm  
177 of FA, the logarithm of DSA and NF (independent variables), while the dependent variable was, in turn,  
178 the richness of: (a) overall *forest-dependent* species; (b) *generalist* species; (c) *edge* species; (d) *interior*  
179 species. We considered as species richness in a fragment the maximum number of bird species (all  
180 together or separately, according to ecological groups) detected inside it. In order to account for the  
181 possible effect of forest management practices on species richness (see Dondina et al., 2015), we  
182 included a two-level independent categorical variable in the models: coppices or high forests. This  
183 information was collected in the field during bird surveys, and refers to the prevailing forest condition  
184 resulting from the management practice in each fragment. One of the most important assumptions of  
185 GLMs is that predictors should not be strongly correlated to each other (Zuur et al., 2009). For this  
186 reason, we checked the pairwise correlation between independent variables using the Spearman  
187 method before running each model. All correlation coefficients were lower than |0.6|. We also verified  
188 that all other GLMs requirements were met by checking diagnostic plots. Finally, in order to evaluate  
189 the goodness of fit of each model, we used the percentage of explained deviance. All the analyses were  
190 performed using R v. 3.1 (R Core Team, 2014).

#### 191 **Species-level analysis**

192 In order to evaluate how fragmentation acts at the single species level, we investigated if particular  
193 combinations of spatial covariates affected species presence probability. To this aim, we used the  
194 Indicator Species Analysis approach (Dufrêne & Legendre, 1997; De Cáceres & Legendre, 2009), which,  
195 calculating an Indicator Value (IndVal) index, allowed us to determine species, or groups of species,  
196 associated to a prior partition of sites. The IndVal index is the product between *specificity* or *positive*



197 *predictive value* (A), that is the probability that a surveyed site belongs to the group of sites where the  
198 target species was found, and *fidelity* (B), that is the probability of finding a target species in sites  
199 belonging to a particular group of sites. We then identified the highest association value between  
200 species and groups of sites using the IndVal index and tested the statistical significance of this  
201 relationship with a permutation test (999 permutations). In order to look for indicator species of both  
202 individual group of sites or a combination of those, we used the method proposed by De Cáceres et al.  
203 (2010), which is an extension of the original IndVal index. In our analysis, we used forest fragments as  
204 sites and we partitioned them in clusters according to their values of FA, DSA and NF, and also their  
205 forest management practice. For this purpose, we categorized each continuous spatial covariate into  
206 two classes, arbitrarily but sensibly chosen. We classified forest fragments into small (S;  $\leq 2$  ha) or large  
207 (L) according to FA; near (N;  $\leq 5$  km) or far (F) according to DSA; and with few (F;  $\leq 5$ ) or many (M)  
208 neighbouring fragments according to NF. By combining the two levels of the four variables (the three  
209 spatial covariates and forest management practice), we obtained 16 clusters. In order to avoid a strong  
210 sample size effect, we considered only the 11 clusters with at least five sampling units, and we analysed  
211 only the 40 species evenly distributed throughout the study area. The Indicator Species Analysis was  
212 performed applying the *multipatt* function implemented in the *indicspecies* package ver. 1.7.1 in R (De  
213 Cáceres & Legendre, 2009).

214 For each species significantly related to a cluster or a group of clusters, besides the values of the  
215 *specificity* (A) and *fidelity* (B), the analysis returns the squared-root of the IndVal index. We then  
216 grouped all the species associated to the same cluster or group of clusters in the same IndVal group of  
217 species.

218

## 219 **RESULTS**

### 220 **Bird survey**

221 From 2007 to 2014, 1462 point counts were performed and 144 bird species were found, 54 of which  
222 were classified as *forest-dependent* species linked to broadleaved or mixed forests. The mean number  
223 of species detected at each point was 11.2 ( $\pm 0.096$  SE), 8.5 ( $\pm 0.081$  SE) of which were forest  
224 dependent. We split the whole set of *forest-dependent* species into three ecological groups: *generalist*  
225 (21 species), *edge* (22 species) and *interior* (11 species). The mean number of species detected at each  
226 point was 5.5 ( $\pm 0.055$  SE) for *generalist* species, 2.3 ( $\pm 0.048$  SE) for *edge* species and 0.8 ( $\pm 0.028$  SE)  
227 for *interior* species.

### 228 **Community level analysis**

229 The GLM applied to the overall *forest-dependent* species richness explained 24% of the variance (Tab.  
230 1). The logarithm of FA did not show any significant effect on *forest-dependent* species richness (Fig.  
231 2a). Conversely, the logarithm of the DSA and NF had a significant negative and positive influence,  
232 respectively (Fig. 2b & 2c). The model also showed that the overall *forest-dependent* species richness  
233 was on average 0.248 (SE = 0.050) higher in high forests than in coppices.

234 Considering the *forest generalist* species richness only, the GLM explained 30% of the variance (Tab.  
235 2). In this case, both the logarithm of FA and NF positively and significantly affected the richness of  
236 *generalist* species (Fig. 2d & 2f). In addition, the logarithm of DSA showed a negative effect (Fig. 2e). In  
237 this case, too, the model revealed a positive association between *generalist* species richness and high  
238 forests, with on average of 0.238 (SE = 0.065) more species than in coppices.

239 The analysis conducted on *forest edge* species richness explained only 7% of the variance (Tab. 3). The  
240 logarithm of FA did not show any significant effect on *edge* species richness (Fig. 2g). Conversely, both  
241 the logarithm of the DSA and NF had a significant positive effect (Fig. 2h & 2i). In this case, the mean  
242 of *edge* species richness in high forests was 0.202 (SE = 0.083) higher than in coppices

243 Taking into account only the richness of *forest interior* species, the explained variance of the model  
244 reached 42% (Tab. 4). Both the logarithm of FA and NF had a positive significant influence on *interior*  
245 species richness (Fig. 2j & 2l), while the logarithm of the distance from the DSA had a negative effect

246 (Fig. 2k). Again, the model revealed a positive association between *interior* species richness and high  
247 forests, but the mean species richness in this type of forest was 1.2 (SE = 0.191) higher than in coppices,  
248 where the estimated mean number of *interior* species was negative (-2.055, SE = 0.173).

### 249 **Species-level analysis**

250 Fifteen of the 40 forest-dependent species considered in the Indicator Species Analysis were found to  
251 be significantly associated with one or more clusters of fragments. Based on their association with one  
252 or more clusters (measured by the IndVal index), we combined the species into 10 IndVal groups (Tab.  
253 5). Eight of these groups were composed only of one species, while the other two were composed of  
254 five and two species, respectively. The specificity, or positive predictive value (A), ranged from 0.32 for  
255 the Common Redstart (*Phoenicurus phoenicurus*) to 0.95 for the Wood Pigeon (*Columba palumbus*),  
256 whereas the fidelity value (B) ranged from 0.15 for the Sparrowhawk (*Accipiter nisus*) to 0.8 for the  
257 Common Redstart. The square-root of the IndVal index ranged from 0.37 for the Sparrowhawk to 0.8  
258 for the Chaffinch (*Fringilla coelebes*). The number of clusters to which the species pertaining to the  
259 same IndVal group were associated varied from a minimum of one (groups 1 and 4) to a maximum of  
260 nine (group 10).

261

## 262 **DISCUSSION**

### 263 **Community level analyses**

264 The application of the IBT in terrestrial contexts, e.g. in forest fragmentation studies, is sometimes  
265 deprecated (Mac Nally, 2007; Sekercioglu & Sodhi, 2007; Laurance, 2008) because most of the  
266 assumptions it requires are often disattended (Watling & Donnelly, 2006). One of the most important  
267 violations results from the application of the IBT to open communities, which typically characterize  
268 terrestrial ecosystems. In this study, in order to remove the blending contribution of co-occurring  
269 species with different ecological traits in defining the habitat "island" fragment richness, we split all

270 the *forest-dependent* species into the following three homogeneous groups: *generalist*, *edge* and  
271 *interior* species. This allowed us to shift from the heterogeneous group of overall *forest-dependent*  
272 species, comparable to an open community, to several homogeneous groups, more similar to closed  
273 communities.

274 As argued above, the application of the IBT to the overall *forest-dependent* species group did not reveal  
275 any significant relationship between its richness and FA. However, the results changed when we split  
276 the overall *forest-dependent* species in the three ecological groups. Species richness was significantly  
277 and positively affected by FA both for the *generalist* group and for the *interior* group. Nevertheless,  
278 the slope of the species-area relationship (Connor & McCoy, 1979; Ricklefs & Lovette, 1999) revealed  
279 that the response of the *generalist* group and the one of the *interior* group were not the same. In fact,  
280 *interior* group showed a marginally significant ( $P < 0.1$ ) steeper slope than *generalist* group, highlighting  
281 that the area effect is stronger for habitat specialists than for generalists (Brotons et al., 2003; Krauss  
282 et al., 2003; Magura et al., 2008), as the first ones can only inhabit fragments larger enough to maintain  
283 a core area. Conversely, *edge* species richness seemed not to be affected by FA, probably because even  
284 small fragments, in which the perimeter/area ratio maximizes the edge density, may prove suitable for  
285 these species.

286 The relationship between species richness and DSA was found to be significantly negative for the  
287 overall *forest-dependent* species, as well as for the *generalist* and *interior* species. In this case, too, the  
288 slope revealed some significant ( $P < 0.05$ ) differences: *interior* species have a steeper slope than both  
289 *generalist* and overall *forest-dependent* species. Being less negatively affected by the matrix, *generalist*  
290 species may better disperse through it, thus partially overcoming the isolation effect (Andrianarimisa  
291 et al., 2000; Renjifo, 2001). In addition, *generalist* species, in contrast with *interior* species, may  
292 maintain metapopulations far from sources areas, since they are able to exploit small forest fragments  
293 which lack in core areas. On the other hand, the negative relationship between the richness of overall  
294 *forest-dependent* species and DSA is not very strong, as it results from the combined response of  
295 species pertaining to different ecological groups with opposite tendencies. Indeed, the *edge* species

296 richness significantly increased with the distance from the identified source areas (i.e. blocks of forest  
297 larger than 1000 ha). Therefore, these sources are likely not to be the real ones for *edge* species. In  
298 fact, as highlighted by Margules & Milkovits (1994) and Laurance et al. (2002), *edge* species increase  
299 dramatically in fragmented landscapes, which probably represent their actual source areas.

300 The richness of overall *forest-dependent*, *generalist*, *edge* and *interior* species was positively influenced  
301 by NF, with similar slopes. However, these relationships have different meanings. For *interior* species,  
302 the higher the number of surrounding fragments is, the greater is the probability to find fragments  
303 that host a core area. Conversely, for *edge* species, what it matters is the increase of edge habitat  
304 availability (Laurance, 2008), which, in turn, is associated with a higher number of surrounding  
305 fragments. Finally, the positive association between *generalist* species and the number of  
306 neighbouring fragments depends on an increase in the overall habitat availability. In addition, all the  
307 three groups of species were positively influenced by the abundance of surrounding fragments, as  
308 these can serve as stepping stones for individual movements in a heavily fragmented landscape (Baum  
309 et al., 2004).

310 Our results confirm that the application of the IBT to terrestrial contexts can lead to misleading  
311 conclusions if we consider the overall species richness without taking into account the different  
312 species' ecological traits. For example, if we had not considered the contribution of species with  
313 different ecological traits to the overall species richness, the species-area relationship it would have  
314 been completely lost. Moreover, as highlighted from other studies (Bani et al. 2006), the results  
315 showed that *interior* species are the ecological group that is more affected by habitat fragmentation.  
316 Therefore, we suggest using the *interior* species richness as an indicator for the effect of fragmentation  
317 when dealing with open communities.

### 318 **Species-level analyses**

319 As abovementioned, species richness might not always be the most valuable proxy for conservation  
320 purposes (Fleishman et al., 2006), even when groups with homogeneous ecological traits are

321 considered, as it does not take into account the biological differences between species. For this reason,  
322 by means of the IndVal analysis, we ascertained how each species may be differently affected by the  
323 degree of fragmentation, according to both its ecological and biological traits. In this way, we were  
324 able to identify species, or groups of species, that could act as indicators for particular combinations  
325 of spatial covariates concerning landscape fragmentation.

326 We considered as useful indicators only the first four IndVal groups of species resulting from our  
327 analysis, as they were associated with no more than 2 of the 11 clusters of fragments. In order to be  
328 considered informative, an indicator, or a group of indicators, should have a significant and relatively  
329 high IndVal index value (Legendre, 2013), but should also be linked to a restricted number of clusters.

330 All the species pertaining to the first four IndVal groups appeared to be associated only with fragments  
331 managed as high forest and located in archipelago contexts with many patches. However, these four  
332 groups differed from each other in their requirements concerning fragment area and distance from  
333 source areas. The most demanding IndVal group only includes the European Nuthatch (*Sitta europaea*).  
334 This species, which is strictly sedentary, has a low dispersal capability and needs large individual  
335 territories, linked to core area habitats (Van Dorp & Opdam, 1987; Matthysen et al., 1995). Its  
336 populations could thus be established only in large fragments, relatively close to source areas (cluster  
337 NLM-H). The second IndVal group of species was also associated to this cluster, although it was also  
338 linked to fragments classified as small (clusters NLM-H and NSM-H). The Common Redstart, the only  
339 member of the third IndVal group, was found to select fragments near a source area, but only small  
340 ones (cluster NSM-H). This is probably due to a preference of this species for heterogeneous mosaics  
341 consisting in an archipelago of patches of mature open forest (Taylor & Summers, 2009), even in  
342 moderately urbanized areas (Droz et al. 2015). The presence of the species pertaining to the second  
343 and third clusters in forest fragments appeared to be limited mainly by dispersal capability, as they  
344 occur only in large or small fragments near source areas. The presence of the species pertaining to  
345 these two groups in fragments near source areas could also be guaranteed in small fragments,  
346 provided they were large enough to allow the establishment of individual territories.

347 Conversely, the presence probability in forest fragments of the Eurasian Wren, representing the fourth  
348 IndVal group, seemed to be mainly limited by the possibility to find core area habitats, which only  
349 occur in large fragments, similarly to the European Nuthatch. Conversely, the Eurasian Wren, seemed  
350 not to be limited by dispersal, as the species occurred both in fragments near or far from source areas  
351 (clusters NLM-H and FLM-H).

352 These results confirmed those obtained from the community-level analysis: all *interior* species are  
353 particularly sensitive to fragmentation, which makes them particularly suitable as indicators. However,  
354 our research demonstrated that, even within this group, different species respond differently to the  
355 degree of fragmentation, according to their biological traits. In particular, the analysis identified three  
356 different groups of *interior* species suitable to be used as proxies in three different landscape contexts.  
357 Moreover, our results highlight that also some species not strictly linked to core areas (the  
358 Sparrowhawk *Accipiter nisus*, the Jay *Garrulus glandarius* and the Common Redstart) have biological  
359 traits that make them useful proxies of fragmentation effects, in the same way as the *interior* species  
360 pertaining to the second IndVal group.

361

## 362 **Conclusions**

363 Our results highlight the strong effect of species' ecological and biological traits on species distribution  
364 in terrestrial ecosystems by means of well-established ecological laws, such as those of the IBT. Indeed,  
365 the species' ecological traits, considered at the community-level analysis, exert a strong influence on  
366 species-area relationships and isolation effects. Compared to other groups of species, such as the  
367 generalist ones, *interior* species are those that better respond to IBT laws, which makes them the best  
368 possible indicators of the effect of fragmentation. Nevertheless, neither all the *interior* species, nor the  
369 *generalist* species have the same ecological meaning. After considering species' biological traits, it was  
370 possible to ascertain how species are differently affected by the IBT spatial covariates. This led to the  
371 identification of area-limited and/or dispersal-limited species, which may serve as indicators for  
372 landscapes with different degrees of fragmentation.

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378

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- 582
- 583
- 584
- 585 **BIOSKETCHES**

586 The Biodiversity Conservation Unit of the Department of Earth and Environmental Sciences at  
587 University of Milano–Bicocca focuses on wildlife–habitat relationships, identification and evaluation of  
588 ecological networks, forest management practices assessment for animal conservation, wildlife  
589 surveys and management, long-term monitoring programs, population and landscape genetics. Author  
590 contributions: O.D. performed statistical analyses and wrote the paper, V.O. performed field survey  
591 and statistical analyses, P.D. performed data analyses and L.B. designed and coordinated the study,  
592 performed field survey and wrote the paper.

593

594 Table 1  
 595 Results of the Poisson GLM performed on the overall *forest-dependent* species richness collected in 344 forest  
 596 fragments in Lombardy administrative region in northern Italy (Explained deviance: 24%).  
 597

Predictors	Slope	SE	z	Pr(> z )
(Intercept)	1.984	0.034	58.391	<0.001
log (Area)	0.018	0.013	1.381	0.167
log (Distance)	-0.029	0.008	-3.531	<0.001
N patches	0.011	0.002	4.754	<0.001
Forest management (high forest)	0.248	0.050	4.967	<0.001

598

599

600 Table 2  
 601 Results of the Poisson GLM performed on the *forest generalist* species richness collected in 344 forest fragments  
 602 in Lombardy administrative region in northern Italy (Explained deviance: 30%).  
 603

Predictors	Slope	SE	z	Pr(> z )
(Intercept)	1.452	0.044	33.015	<0.001
log (Area)	0.036	0.017	2.122	0.034
log (Distance)	-0.064	0.010	-6.141	<0.001
N patches	0.009	0.003	3.112	0.002
Forest management (high forest)	0.238	0.065	3.654	<0.001

604

605

606 Table 3  
 607 Results of the Poisson GLM performed on the *forest edge* species richness collected in 344 forest fragments in  
 608 Lombardy administrative region in northern Italy (Explained deviance: 7%).  
 609

Predictors	Slope	SE	z	Pr(> z )
(Intercept)	1.046	0.057	18.345	<0.001
log (Area)	-0.014	0.021	-0.712	0.477
log (Distance)	0.058	0.014	4.070	<0.001
N patches	0.009	0.004	2.659	0.008
Forest management (high forest)	0.202	0.083	2.434	0.014

610

611

612

613 Table 4  
 614 Results of the Poisson GLM performed on the *forest interior* species richness collected in 344 forest fragments in  
 615 Lombardy administrative region in northern Italy (Explained deviance: 42%).  
 616

Predictors	Slope	SE	z	Pr(> z )
(Intercept)	-2.055	0.173	-11.908	<0.001
log (Area)	0.171	0.066	2.562	0.010
log (Distance)	-0.273	0.038	-7.173	<0.001
N patches	0.027	0.010	2.774	0.005
Forest management (high forest)	1.200	0.191	6.261	<0.001

617  
 618

619

620 Table 5.  
 621 The 15 species, combined in 10 IndVal groups, significantly associated with one or more of 11 out of 16 potential clusters of fragments (8 spatial clusters x 2 forest management  
 622 types). For each cluster of fragments, the forest management type is specified after the acronym: high forest (-H) or coppice (-C) (see Figure 3 for the spatial clusters acronyms).  
 623 For each species, the specificity value (A), fidelity value (B) and square-root of the IndVal index, with its significance, are shown.

IndVal group of species	Species	Ecological group	A : specificity value	B: fidelity value	IndVal		Clusters of Fragments											
					Index square-root	Index p-value	NLM-H	NSM-H	FLM-H	NLM-C	NLF-C	NSM-C	NSF-C	FLM-C	FLF-C	FSM-C	FSF-C	
1	<i>Sitta europaea</i>	Interior	0.75	0.33	0.50	0.005	+											
	<i>Accipiter nisus</i>	Generalist	0.88	0.15	0.37	0.045	+	+										
	<i>Certhia brachydactyla</i>	Interior	0.86	0.31	0.51	0.004	+	+										
2	<i>Erithacus rubecula</i>	Interior	0.77	0.54	0.64	0.001	+	+										
	<i>Poecile palustris</i>	Interior	0.71	0.58	0.64	0.001	+	+										
	<i>Garrulus glandarius</i>	Generalist	0.63	0.54	0.58	0.002	+	+										
3	<i>Phoenicurus phoenicurus</i>	Generalist	0.32	0.80	0.50	0.008		+										
4	<i>Troglodytes troglodytes</i>	Interior	0.55	0.33	0.43	0.048	+			+								
5	<i>Cyanistes caeruleus</i>	Generalist	0.74	0.35	0.51	0.018	+	+	+	+					+			
	<i>Aegithalos caudatus</i>	Generalist	0.87	0.33	0.54	0.006	+	+	+	+	+				+			
6	<i>Muscicapa striata</i>	Generalist	0.75	0.36	0.52	0.021	+	+	+	+	+				+			
7	<i>Fringilla coelebs</i>	Generalist	0.85	0.74	0.80	0.001	+	+	+	+	+	+	+				+	
8	<i>Columba palumbus</i>	Generalist	0.87	0.50	0.66	0.009	+	+	+	+	+					+	+	
9	<i>Phasianus colchicus</i>	Edge	0.95	0.27	0.51	0.021	+	+		+					+	+		+
10	<i>Luscinia megarhynchos</i>	Edge	0.92	0.62	0.75	0.001	+	+	+			+			+	+	+	+

624



625 Figure 1  
626 On the left, the location of study area in northern Italy. On the right, the study area with broadleaved forest  
627 cover in the background. Forest source areas (i.e. patches larger than 1000 ha) in black; forest fragments in grey.

628

629

630

631 Figure 2

632 Relationships between the residuals of the logarithm of Fragment Area, logarithm of the Distance from the  
633 nearest Source Area, and Number of neighbouring Fragments and forest bird species richness. On the y axis, the  
634 species richness values predicted by the Poisson GLM. Panels a), b) and c): overall species richness. Panels d), e)  
635 and f): *generalist* species richness. Panels g), h) and i) *edge* species richness. Panels j), k) and l) *interior* species  
636 richness. For each graph the  $R^2$  and the significance of the model are provided.

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640 Figure 3.

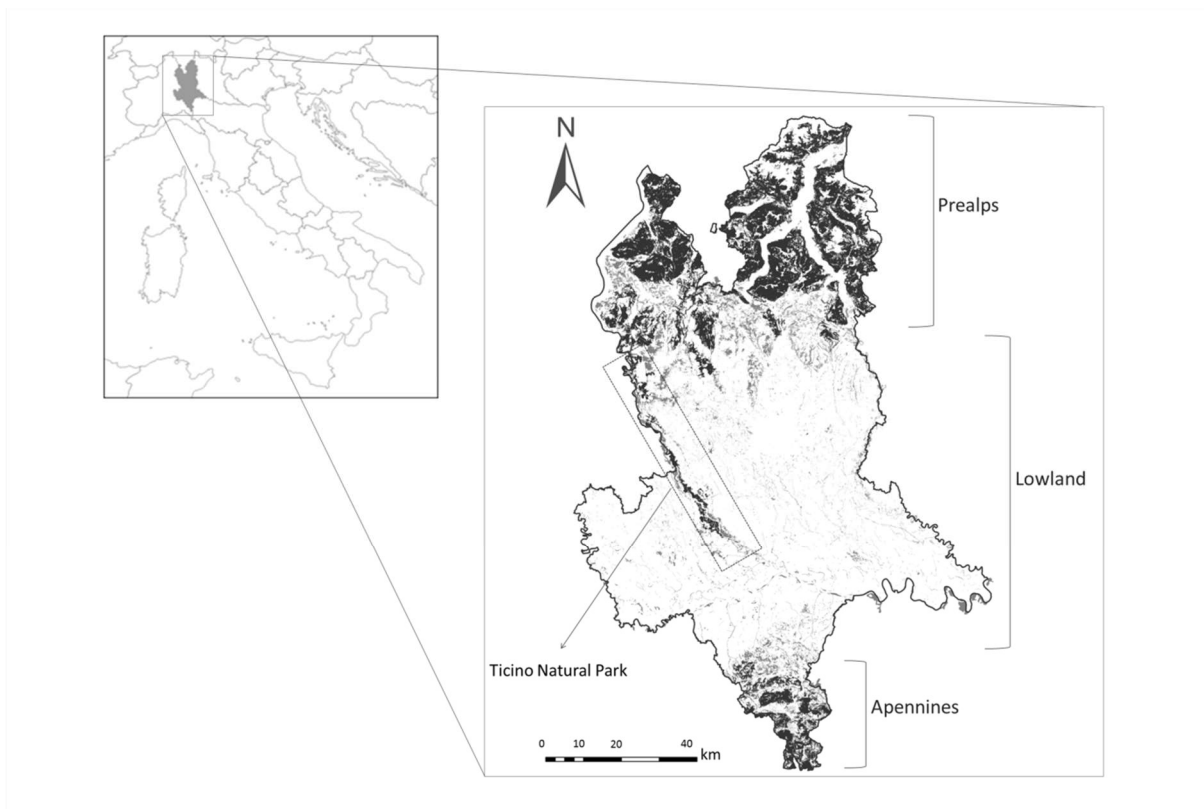
641 The 8 clusters of fragments, resulting from the combination of the two-levels three spatial covariates. On the  
642 left, in grey, source area, Black dots; focal fragment for which spatial covariates are referred; Grey dots:  
643 surrounding fragments; NLM: fragments near (N) to the source area, Large in size (L), and with Many (M)  
644 surrounding fragments; NSM: fragments near (N) to the source area, Small in size (S), and with Many (M)  
645 surrounding fragments; NLF: fragments near (N) to the source area, Large in size (L), and with Few (F) surrounding  
646 fragments; NSF: fragments near (N) to the source area, Small in size (S), and with Few (M) surrounding fragments;  
647 FLM: fragments near (F) to the source area, Large in size (L), and with Many (M) surrounding fragments; FSM:  
648 fragments near (F) to the source area, Small in size (S), and with Many (M) surrounding fragments; FLF: fragments  
649 near (F) to the source area, Large in size (L), and with Few (F) surrounding fragments; FSF: fragments near (F) to  
650 the source area, Small in size (S), and with Few (M) surrounding fragments.

651

652

653 Figure 1

654

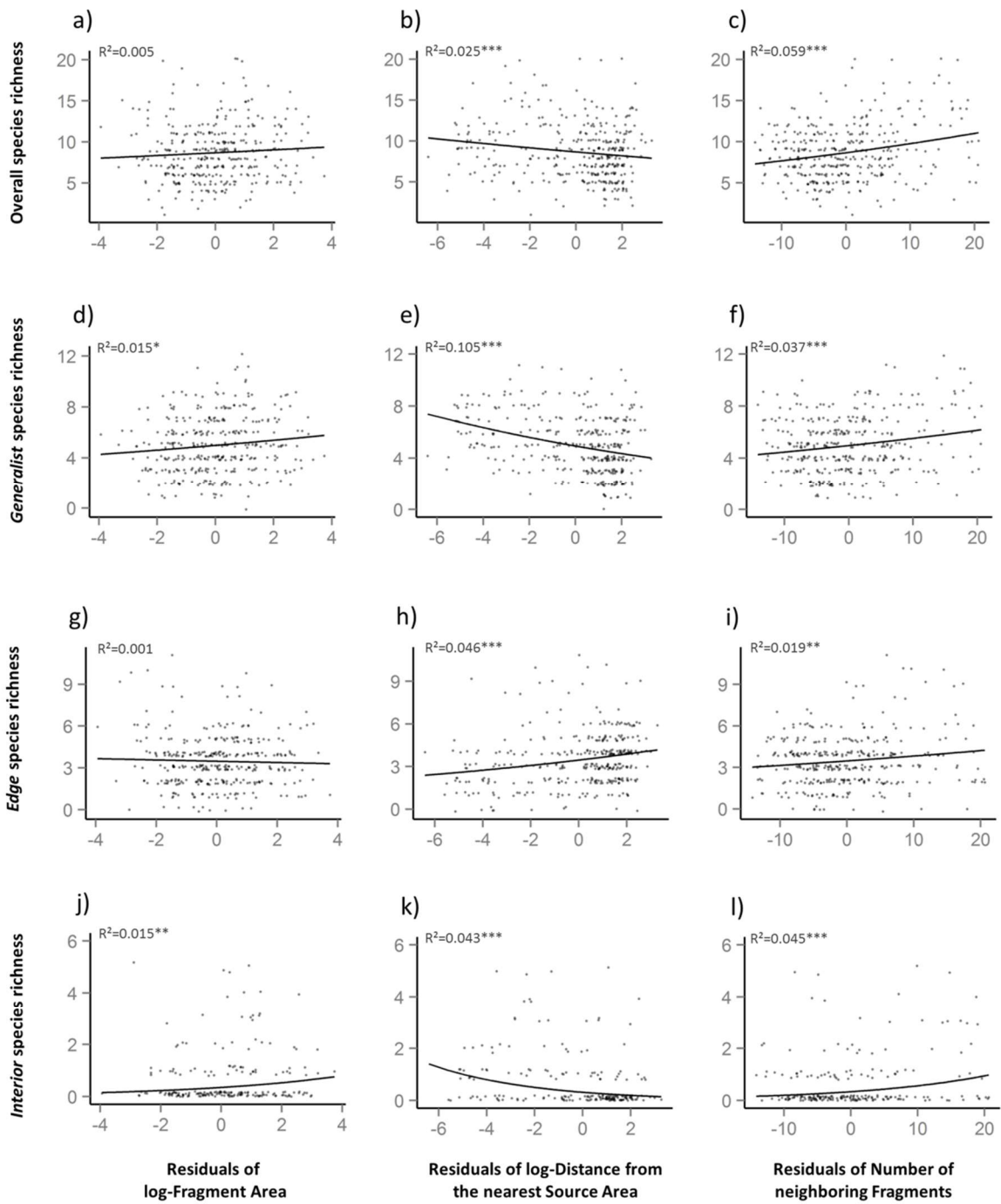


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657 Figure 2

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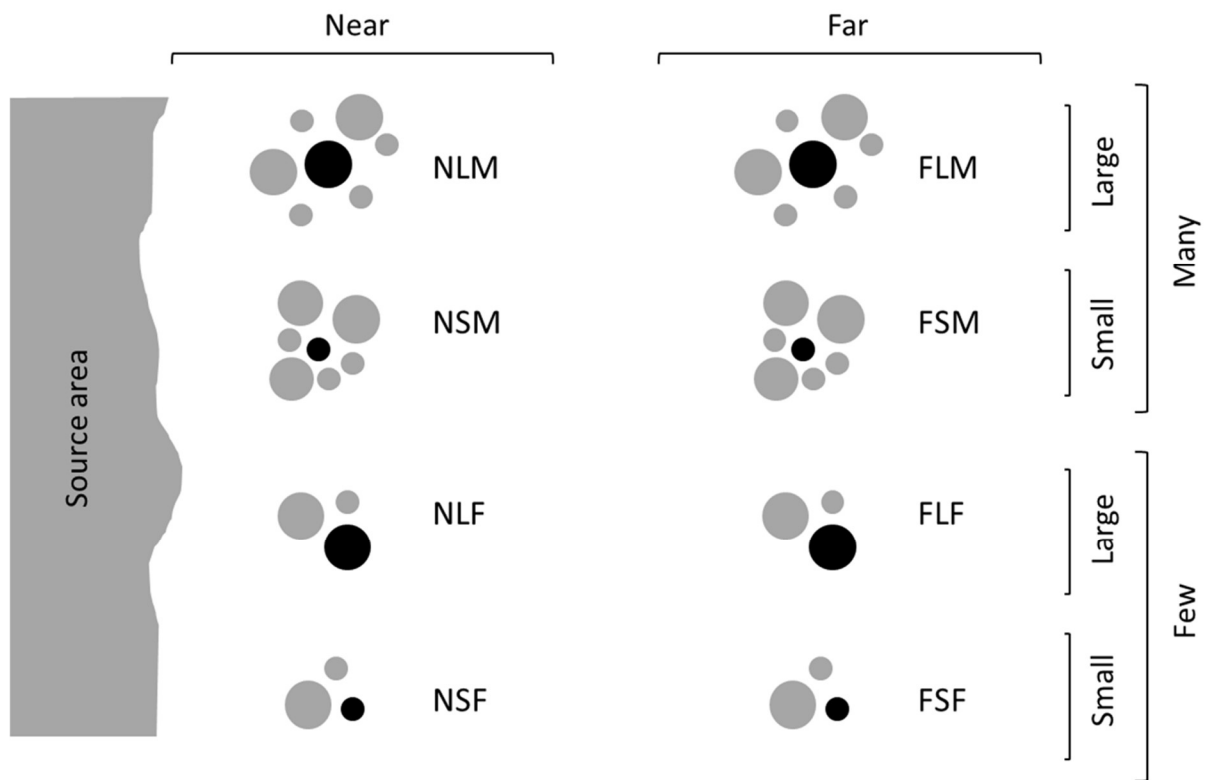


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661 Figure 3

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