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Bird communities of a temperate forest: spatio-temporal partitioning between resident and migratory species

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1 **ABSTRACT**

2 A lot of bird species are declining in Europe and studies of bird community assembly are
3 fundamental to propose efficient conservation actions. Many studies were carried out on the
4 regional variability of abundance and distribution of bird communities, but few studies
5 considered the local patch variability. In this study, we worked on intra-patch variability of
6 breeding bird community in the forest patch of Corbière (Britanny, France). We tested
7 whether bird community distribution was related to habitat characteristics and whether
8 distribution patterns depended on life history traits of species. During three years, we used a
9 regular sampling and the point count method to sample whole bird community within this
10 forest patch. Our results showed that several biotic and abiotic variables - distance to forest
11 edge, deciduous tree cover, coppice cover, elevation - controlled individual abundances of
12 bird species as well as indicators of bird community - abundance, diversity, evenness.
13 Moreover, we found that abundances of resident birds, short-distance migrants and long-
14 distance migrants were differently related to biotic and abiotic variables, and that these
15 relationships varied within the breeding season. We suggest that this space partitioning may
16 be explained by the temporal dynamics of the bird community: resident and short-distance
17 species were present earlier than long-distance species in the forest patch, and might
18 preferentially choose high quality habitats. Long-distance migrants arrived later in the
19 breeding season and might not find the same habitat availability, they might consequently
20 only nest close to the forest edge, in high sites or sites with sparse understory. Our results
21 show that local studies, taking into account migratory status and species dynamics at intra-
22 season scale, are important keys to understand distribution patterns which are observed along
23 entire breeding seasons.

24 **Keywords:** forest biodiversity, bird community, species partitioning, migratory status,
25 temporal dynamics

26 INTRODUCTION

27 The study of bird communities is often used to determine indicators of health of natural
28 habitats under global changes (Canterbury *et al.* 2000, Gregory *et al.* 2007). Specifically,
29 studies of bird communities permit identification of population trends: for instance, Gregory
30 *et al.* (2007) found a sharp decline (-13 % over the period 1990-2002) of forest birds in
31 Western Europe. Population trends may depend on life history traits of species: Julliard *et al.*
32 (2003) and Jiguet *et al.* (2007) showed, noteworthy, the decline of specialist species – in
33 France, this decline is moderate in protected areas but is accentuated in areas without special
34 status (Devictor *et al.* 2007). Moreover, it has been shown that among European forest birds,
35 long-distance migrants declined more strongly than short-distance migrants or permanent
36 residents (Sanderson *et al.* 2006, Gregory *et al.* 2007). Arrival dates of migratory birds
37 became earlier in recent decades, in particular for early migratory species (Tryjanowski *et al.*
38 2005), as did the starting dates for fall migration of long-distance migrants (Jenni & Kéry
39 2003) and broods production (Both & Visser 2001). Overall, global changes have strong
40 effects on bird communities, and these effects depend on ecology and life history traits of bird
41 species, especially their breeding phenology. As efficient practices of protection and
42 conservation became crucial for maintaining avian biodiversity, we need to understand the
43 mechanisms driving local bird abundance and distribution (Raymond *et al.* 2010, Balestrieri
44 *et al.* 2015). According to studies at regional scales, forest bird communities can be driven by
45 deterministic or random processes (Renner *et al.* 2014) and many studies were already
46 conducted at this scale to identify deterministic processes, *i.e.* biotic and abiotic factors
47 governing distribution of forest bird communities, such as forest composition and structure,
48 and amount and nature of forest edges (Martin-Morales 2005, Goetz *et al.* 2010).

49 First, tree species composition and structure of forest patch drive bird community distribution.

50 The density and age of trees can determine community species richness (James & Warner

51 1982, Berg 1997, Poulsen 2002). Spatial heterogeneity of tree species distribution may
52 increase overall bird abundance and increase abundance of specific functional groups
53 (Freemark & Merriam 1986). Moreover, the composition of forest stands - deciduous *vs*
54 coniferous dominance - is a very important factor in habitat selection by species, since many
55 species have distinct habitat and resource preferences (James & Wamer 1982, Patterson &
56 Best 1996, Berg 1997). More recent studies also showed that heterogeneity of vertical
57 structure and height of canopy can increase the richness of migratory birds (Goetz *et al.* 2007,
58 2010). Finally, available resources, often related to moisture in forest habitats due to tree
59 density (Petit *et al.* 1985), and forest productivity may increase bird species richness (Cody
60 1981, Böhm & Kalko 2009).

61 Second, the amount and nature of forest edges drive bird community distribution. It has been
62 shown that the amount of edges, subject to higher predation and parasitism, could reduce
63 overall avian biodiversity in forest patches and strongly decrease abundance of specific
64 functional groups preferring forest core (Herkert 1994, Deng & Gao 2005, Ludwig *et al.*
65 2012). There may, however, exist some species preferring the edge, mainly depending on
66 their diet (Kroodsma 1984, McCollin 1998, Martinez-Morales 2005). Overall, the role of
67 edges has been importantly debated in ecology and if their negative impact of avian
68 biodiversity has been recognized, a consensus assessed that edge effects strongly depend on
69 the matrix surrounding the forest patch (Donovan *et al.* 1997). Noteworthy, the contrast
70 between forest resources and landscape resources (Ries & Sisk 2004) and the specific
71 interactions between forest species and openfield species (Fagan *et al.* 1999) are important
72 drivers of edge effect on bird communities.

73 We observe very different responses of bird communities to the previously-listed habitat
74 factors according to life history traits of bird communities (Lynch & Whigham 1984, Estades
75 & Temple 1999, Hansbauer *et al.* 2010, Gharehaghaji *et al.* 2012). Life history traits illustrate

76 ecological strategy of species to respond to biotic and abiotic conditions, and permit a
77 mechanistic understanding of the relationships between environmental factors and species
78 distribution (Caprio *et al.* 2008). Clearly, the migratory status - resident, short and long-
79 distance migrant - is an important trait of bird species, which can explain spatial distribution
80 patterns of bird communities (Lynch & Whigham 1984, Flather & Sauer 1996, Korňan *et al.*
81 2013). Resident and migratory species have indeed different periods of presence in forest
82 patches and thus different temporal dynamics, which lead to different spatial distributions and
83 to seasonal variation in spatial distributions (Griffis-Kyle & Beier 2005, Böhm & Kalko
84 2009).

85 Most studies on breeding bird distribution in wooded areas focused on landscape or regional
86 scale. At these scales, inter-patch comparisons (size, shape, composition) were designed to
87 explain the variability of bird communities between patches. However, efficient conservation
88 practices often occur at local scale, which is the scale on which management projects are the
89 more easily carried out. Studies looking for mechanisms driving bird distribution at intra-
90 patch scale are scanty (Proença *et al.* 2010, Albanese & Davis 2015, Isotti *et al.* 2015).
91 Furthermore, few studies considered the temporal dynamics depending on the migratory
92 status of species, despite this status was often studied at larger scales. In this study, we
93 proposed to analyse within a same forest patch the relationships between bird species
94 distribution and environmental variables (habitat characteristics) in connection with bird
95 migratory status and intra-season dynamics. Based on previously published work, we
96 addressed the following questions: (i) Do environmental variables explain the distribution of
97 bird species? (ii) Do the distribution patterns depend on the migratory status of species? (iii)
98 Do the distribution patterns vary within the breeding season? We used the point count method
99 to sample the whole bird community of the forest patch of Corbière (Britanny, France), during
100 three years, and using a regular seasonal sampling procedure. We collected a full set of

101 relevant environmental variables and tested relationships between bird community and
102 environmental variables, at different times of the breeding season and depending on the
103 migratory status of species.

104 **MATERIALS AND METHODS**

105 *Study area*

106 The study was carried out in the forest patch of Corbière, located 15 kilometers east of the
107 city of Rennes, Brittany, France (48° 14'N, -1° 39'W) and extending 740 hectares (Figure 1).
108 The study area is the property of "Conseil Départemental d'Ille-et-Vilaine" who issued
109 permission for field surveys. This study involved protected species (passerine community) but
110 was only based on audiovisual observations and did not require any official authorization nor
111 ethic committee statements. The forest patch is surrounded by a typical Breton agricultural
112 landscape, which has undergone significant land reparation but retains a high degree of
113 heterogeneity. It is a mixed temperate forest mainly composed of deciduous trees belonging
114 principally to *Quercus petraea* and *Quercus pedunculata* series. There is a wide range of
115 ecological conditions, especially related to local topography, forest stands and local
116 management – management depends on the owners of the forest stands and is, overall, few
117 intensive.

118 *Composition and abundance of bird community*

119 The study focused on the forest breeding bird community during the nesting period extending
120 from April to June. The sampling period was in accordance with recommendations of Ralph
121 *et al.* (1995). It involved all potentially breeding bird species in the forest patch so it was
122 mainly based on the community of passerines (see Appendix 1) with mainly understory
123 nesters. Data were collected by the method of point counts (e.g. Holmes *et al.* 1986). A grid
124 with a mesh size of 500 m was positioned on the forest, and 29 bird point counts were

125 regularly distributed on the mesh grid to cover the entire forest patch (Figure 1). As one year
126 of study appears insufficient to validate habitat/species relationships (Adamik & Kornan
127 2004), we performed the study over 3 years, from 2008 to 2010, with three field sessions at
128 each spring (once per month: April, May, June) to accurately describe the breeding bird
129 community at each point count. During the three annual field sessions, the 29 point counts
130 were sampled within 3 hours from sunrise with a period of listening and observation of 15
131 minutes at each point, in standardized surveys conditions. All encountered species were
132 recorded, by taking into account only encounters with different individuals, according to the
133 following nomenclature: 1 for songbirds, couples, occupied nests and family groups, and 0.5
134 for solitary birds seen or heard (songs or calls), to take into account that some birds may be
135 migrating or passing by and did not belong to the local community. We assigned the
136 migratory status of bird species - residents, short-distance migrants and long-distance
137 migrants - using the atlas of Dubois *et al.* (2008) and “Groupe ornithologique Breton” (2012).

138 *Composition and structure of forest patch*

139 The Office National des Forêts (ONF) conducted a complete mapping of the forest in the
140 massif of Corbière in 2007, concerning forest stands and habitats: tree species composition,
141 coppice cover, number of dead trees and cavities as well as information on the forest structure
142 with the basal area (reflecting the density and age of the grove, *i.e.* the sum of the surfaces of
143 each section of tree at 1.30 meter above the ground, in m²/ha). The distribution of stands
144 dominated by deciduous or coniferous trees within the forest patch is shown on Figure 1. A
145 Digital Terrain Model (DTM) was performed to describe patch topography, giving us a
146 quantitative elevation variable at each point count (Figure 1). All information were compiled
147 with a GIS (Geographic Information System, ArcGIS 10 software). Then, we used a buffer of
148 200 m radius to quantify the previously-listed environmental variables around the point
149 counts. We also calculated a distance to the forest edge for each point count. Finally, we

150 calculated an heterogeneity index of the tree composition around the point counts; this index
151 was based on the cumulative stand area distribution and was interpreted as the probability that
152 two randomly chosen pixels in the patch were not situated in the same stand (DIVISION
153 index, software Fragstats 4.1., McGarigal *et al.* 2012). All variables used in analyses are
154 shown in Appendix 2.

155 *Data analysis*

156 Prior to analyses we center-reduced all data, *i.e.* transformed variables by subtracting their
157 mean and dividing by their standard deviation, as it ensures regression coefficients are
158 comparable among models. First, we performed a co-inertia analysis (Chessel *et al.* 2003) to
159 evaluate relationships between distribution of individual bird species and environmental
160 variables. To conduct this analysis, we used a matrix of cumulative maximal abundances, *i.e.*
161 containing for each point count the sum of the maximal abundances observed for each species
162 during the three years; maximal abundances at each year were obtained using the highest
163 abundance observed along the three annual surveys (April, May, June). Only 35 out of the 54
164 bird species recorded were considered for this co-inertia analysis, to exclude very rare species
165 that would affect the analysis disproportionately to their abundance (the criteria was species
166 present in less than 3 among the 29 point counts). To perform the co-inertia analysis, a
167 factorial correspondance analysis (COA) was first performed on the matrix of cumulative
168 maximal abundances, then, a principal component analysis (PCA) weighted by the lines of the
169 COA (Chessel *et al.* 2003) was carried out on the matrix of environmental variables—
170 excluding redundant environmental variables after prior selection on the matrix of
171 correlations. The co-inertia analysis was finally performed to evaluate covariation between
172 COA and PCA.

173 Then, we used mixed models (see Zuur *et al.* 2009) to explain bird community indicators
174 (total abundance, diversity, evenness, abundance of residents, short-distance migrants and
175 long-distance migrants) by environmental variables and month of the breeding season. We
176 used for each month the sum of abundances observed during the three years. Environmental
177 variables were the fixed effects, and month was the random effect – i.e. a 3-level random
178 effect, which is relevant for a random effect (Gelman & Hill 2007). For each dependent
179 variable, we constructed an initial model containing all the fixed effects and the random effect
180 (fixed effects: distance to edge, coniferous tree cover, deciduous tree cover, coppice cover,
181 elevation, heterogeneity, basal area; random effect: month), and we optimized the model
182 using a backward stepwise selection procedure of explanatory variables, keeping the
183 significant variables only. Random effects were significant when their range of values, i.e.
184 lower/estimate/upper, excluded the zero value. We used the “nlme” package under R
185 software. The best model was selected based on AIC and BIC (Burnham & Anderson 2002;
186 Chen & Chen 2008). We tested spatial dependency of residuals using Moran's I, and all
187 results, despite a slight trend of overdispersion, were non-significant.

188 Finally, we used multiple ordinary least square regression models to test the relationship
189 between environmental variables and abundances of residents, short-distance migrants and
190 long-distance migrants, at each month of the breeding season. For each dependent variable,
191 we constructed an initial model containing all independent variables, and we optimized the
192 model using a backward stepwise selection procedure of explanatory variables. We tested
193 spatial dependency of residuals using Moran's I, and all results were clearly non-significant.
194 Here and in previous analyses, distribution of bird community indicators fulfilled normality
195 and homogeneity, we also graphically explored residuals using probability plots and predicted
196 *vs* residual plots and residuals fulfilled normality and homogeneity. All statistical analyses
197 were performed with R 3.3.1 software (R Development Core Team, 2016).

198 **RESULTS**

199 *Relationship between individual abundance of bird species and environmental variables*

200 Co-inertia analysis (Figure 2) was highly significant ($P=0.001$), with a correlation coefficient
201 $RV=0.50$, and the two first axes supported 62% of the total variance of the original two
202 matrices. This indicates that several variables explained bird species distribution. These
203 variables were the deciduous or coniferous tree cover (first axis), elevation (first axis),
204 distance to forest edge, basal area, coppice cover and heterogeneity of tree composition
205 (second axis). For instance, we observed that basal area increased abundance of the Eurasian
206 Sparrowhawk (*Acni*). Meanwhile, the distribution of the Middle Spotted Woodpecker (*Deme*)
207 was influenced by deciduous trees, like the Short-toed Treecreeper (*Cebr*) and the Eurasian
208 jay (*Gagl*). We also observed that when distance to forest edge increased, abundance of
209 migratory species like the Eurasian Golden Oriole (*Oror*) and the Garden Warbler (*Sybo*)
210 declined. The Tree Pipit (*Antr*) and the Common Chiffchaff (*Phco*) principally followed
211 coniferous tree cover, whereas the Common Firecrest (*Reig*) responded strongly to the
212 coppice cover and the heterogeneity of tree composition.

213 *Effect of environmental variables on bird community structure*

214 Various environmental variables significantly explained bird community indicators, and
215 strongly explained abundance of residents, short-distance migrants and long-distance migrants
216 (R^2 ranging from 0.26 to 0.45, Table 1). The month of sampling - random effect - significantly
217 influenced total abundance of bird community as well as abundance of residents and long-
218 distance migrants. This indicates, across the entire forest patch, intra-month and inter-month
219 differences in total abundance of bird community and abundance of residents and long-
220 distance migrants. Distance to edge decreased total abundance and diversity of bird
221 community, as well as abundance of short-distance migrants. Deciduous tree cover increased

222 total abundance and diversity of bird community. Elevation decreased evenness of bird
223 community, and was also the variable that discriminated the most bird abundances depending
224 on migratory status: elevation decreased abundance of residents, while it did not change
225 abundance of short-distance migrants, and increased abundance of long-distance migrants
226 (Fig. 3). Also, basal area decreased abundance of short-distance migrants. Finally, coppice
227 cover decreased abundance and diversity of bird community, and decreased abundance of
228 short-distance migrants. Overall, we observed that abundances of residents, short-distance
229 migrants and long-distance migrants were differently related to environmental variables.

230 *Distribution patterns of residents, short and long-distance migrants along the breeding*
231 *season*

232 Within the three months of the breeding season, environmental variables well explained
233 abundances of residents, short-distance migrants and long-distance migrants (R^2 ranging from
234 0.10 to 0.38, Table 2). The distribution pattern of short-distance migrants was quite the same
235 along the breeding season: for all months of the season, abundance of short-distance migrants
236 decreased with distance to edge and coppice cover (Table 2, Figure 4). Meanwhile, abundance
237 of residents and long-distance migrants showed different distribution patterns along the
238 breeding season (Table 2, Figure 4). From graphical illustrations in Figure 3, we learned more
239 from the random effect of the month we observed in the mixed models, since we observed
240 that abundances of residents were higher at the two first months of the breeding season (April
241 and May), while abundances of long-distance migrants were higher at the two last months of
242 the breeding season (May and June). Abundances of short-distance migrants remained quite
243 the same along the entire breeding season, consistently with the non-significance of the
244 random effect of the month in the mixed model (see Tab. 1). Overall, we observed that three
245 of the six variables influencing abundance of both residents and short-distance migrants
246 within the breeding season, acted with the same sign on these abundances (distance to edge,

247 deciduous tree cover, coppice cover). Consequently, at the middle of the breeding season
248 (May), residents and short-distance migrants displayed very similar responses to
249 environmental variables. On the other hand, three of the six variables influencing long-
250 distance migrants within the breeding season acted with an opposite sign on abundance of
251 residents or short-distance migrants (distance to edge, elevation, heterogeneity)

252 **DISCUSSION**

253 *Environmental variables drove bird species distribution*

254 We showed that bird species distribution strongly depended on environmental variables,
255 which were coniferous or deciduous tree cover, distance to forest edge, elevation and basal
256 area. Our results show that at intra-patch scale, distribution patterns can be deterministic and
257 not stochastic, like observed in some studies (Renner *et al.* 2014). Some species had a clear
258 preference for high zones (European Turtle Dove) or low zones (Middle-Spotted
259 Woodpecker), coniferous zones (Tree Pipit, Crested Tit) or deciduous zones (Shy Jay, Short-
260 toed Treecreeper), forest edges (Eurasian Golden Oriole, Garden Warbler) or forest core
261 (Great-Spotted Woodpecker, Goldcrest). In contrast, other generalist species such as the
262 Common Chaffinch or European Robin were present and equally abundant in all point counts.
263 Overall, these relationships probably resulted from habitat selection of bird species, which
264 depended on the precise ecological traits of each species (foraging, use of strata, nesting,
265 migration). Our results are hence consistent with studies showing, for instance, an effect of
266 edge (Kroodsma 1984, Ludwig *et al.* 2012) or composition of the forest stand (Patterson &
267 Best 1996, Castaño-Villa 2014) on individual bird species distribution. Finally, we observed
268 that variables driving distribution patterns at intra-patch scale may be similar to variables
269 acting at regional scale (Korňan *et al.* 2013) but may act in very different ways on bird
270 species distribution.

271 *Environmental variables explained bird community structure*

272 We also observed that indicators of bird community structure were related to environmental
273 variables. Specifically, we showed that elevation decreased evenness of bird community,
274 indicating high zones harbored more rare species. A consistent result was found in a forest
275 mosaic in northern Europe by Luoto *et al.* (2004), where bird species richness was greater in
276 forests with steep topography. This result is also consistent with general theories in ecology
277 assessing that a tridimensional habitat improves biodiversity, by improving the number of
278 available niches, and consistent with studies on altitudinal gradient assessing an increase of
279 species richness with slight elevation (Loiselle & Blake 1991, Grytnes & Vetaas 2002).
280 Moreover, deciduous tree cover increased abundance and diversity of bird community. We
281 might propose that deciduous zones provided a range of habitats and resources which was
282 larger than that of coniferous zones. Also, coppice cover decreased abundance and diversity
283 of bird community, suggesting birds preferred clear zones with sparse understory to nest.
284 Finally, distance to edge decreased abundance and diversity of bird community. This last
285 result indicates that bird community benefited from the proximity of forest edge, and hence
286 indicates a positive edge effect. This result challenges the frequent observations of negative
287 edge effects at the landscape scale (Rodewald 2002, Batary & Baldi 2004, Deng & Gao 2005,
288 Ludwig *et al.* 2012). From other studies (Penhollow & Stauffer 2000, Bulluck & Rowe 2006,
289 Vetter *et al.* 2013), we might suggest that the forest edge, surrounded by an agricultural
290 landscape which conserves a high degree of heterogeneity, was a zone of high ecological
291 diversity and biotic interactions rather than a zone of high perturbation.

292 *Spatial partitioning between resident and migratory birds*

293 Our results clearly showed a spatial partitioning between resident and migratory birds. Short-
294 distance migrants were located mainly close to the forest edge, in sites with sparse understory

295 and low tree density. Residents preferred low sites, whereas long-distance migrants preferred
296 high sites. Local environmental factors play therefore an important role for habitat selection in
297 bird species depending on the migratory status of species. These results are new because no
298 study, to our knowledge, showed an influence of phenology on habitat selection at intra-patch
299 scale. The positive edge effect observed on abundance of short-distance migrants contradicts
300 previous studies at the regional scale which found that fragmentation, resulting in increased
301 forest edges, decreased migratory species richness (Robinson *et al.* 1995). Meanwhile, a
302 modeling approach employed by Goldstein *et al.* (2003) concluded that maximum richness of
303 migratory species was achieved with an intermediate level of fragmentation, and Gates &
304 Giffen (1991) showed the concentration of migratory birds at edges adjacent to ecotones
305 (riparian zones). Goetz *et al.* (2010) also demonstrated the importance of structure and canopy
306 height to explain migratory species richness. Overall, we hence note that numerous factors
307 could explain the positive edge effect we found for short-distance migrants, and it would be
308 an interesting perspective to study whether the matrix surrounding the forest patch may drive
309 this edge effect. It would be also interesting to test whether differential habitat selection
310 between migratory and resident birds could be used as a proxy for evaluating impacts of
311 habitat fragmentation (Fahrig 1997, Fahrig 2003, Ribeiro *et al.* 2009, Lindenmayer & Fischer
312 2013).

313 *Temporal dynamics of resident and migratory birds*

314 We found that the relationships between environmental variables and abundance of residents
315 and long-distance migrants changed along the breeding season, while relationships between
316 environmental variables and short-distance migrants persisted. Moreover, abundance of short-
317 distance migrants was stable during the breeding season, while abundance of residents
318 decreased at the last month of the breeding season and abundance of long-distance migrants
319 increased from the second month. Thus, these results suggest a temporal dynamics of resident

320 and migrant bird distribution, which could explain their spatial partitioning at the scale of the
321 entire breeding season as well as the spatial structure of entire bird community. Long-distance
322 migrants arrived indeed in the forest patch later than residents and short-distance migrants, in
323 particular because presence of residents within the forest patch could be quite continuous
324 during the year. Overall, distribution patterns of residents were closer to distribution patterns
325 of short-distance migrants than those of long-distance migrants. Therefore, long-distance
326 migrants might not find the same availability of habitats, and nested in zones less occupied by
327 residents and short-distance migrants. An opposite result was found at inter-patch scale by
328 Mönkkönen *et al.* (1990) and Thomson *et al.* (2003), who found the existence of an
329 heterospecific attraction resulting in migratory species choosing habitat patches with many
330 resident species, whose presence is interpreted as a signal of high habitat quality. Overall, if it
331 had already been shown that habitat preferences of bird communities could vary seasonally
332 between breeding season in spring and the beginning of autumnal migration (Murcia 1995,
333 Griffis-Kyle & Beier 2005, Böhm & Kalko 2009, Keller *et al.* 2009, Naoe *et al.* 2011), no
334 study had yet taken into account intra-season dynamics of bird distribution and the role of
335 functional groups of migratory and resident birds in this dynamics. Thus, our results are novel
336 and highlight the importance of accounting for spatio-temporal distribution patterns at fine
337 scale.

338 **CONCLUSION**

339 Our study showed at intra-patch scale that environmental variables (distance to edge,
340 deciduous tree cover, elevation, coppice cover) drove individual bird species distribution as
341 well as bird community indicators (abundance, diversity, evenness). Moreover, abundances of
342 residents, short-distance migrants and long-distance migrants were differently related to
343 environmental variables, in particular in regard to distance to forest edge, tree density,
344 coppice cover and elevation. We also found that spatial distribution of bird species changed

345 during the breeding season, depending on the migratory status of species. Specifically, we
346 observed that, within the breeding season, distribution patterns of short-distance migrants
347 were closer to distribution patterns of residents than to distribution patterns of long-distance
348 migrants. Overall, long-distance migrants arrived later than residents and short-distance
349 migrants in the breeding season, and it might explain the spatial partitioning we observed
350 between resident and migrant birds as well as the structure of the entire bird community: long-
351 distance migrants might not find the same availability of high quality habitats, and might be
352 forced to fall back on still available or low quality ones. These results show the importance of
353 taking into account functional traits of bird species, especially migratory status, and intra-
354 season temporal dynamics to study and understand the distribution patterns of bird
355 communities. Such results may have implications for forest management, to optimize species
356 assemblages and hence the conservation of avian biodiversity in temperate forest
357 environments.

358

359 **REFERENCES**

360 Adamík P, Kornan M (2004) Foraging ecology of two bark foraging passerine birds in an old-
361 growth temperate forest. *Ornis Fennica* 81:13-22.

362 Albanese G, Davis CA (2015) Characteristics within and around stopover wetlands used by
363 migratory shorebirds: Is the neighborhood important? *The Condor* 117:328-340.

364 Balestrieri R, Basile M, Posillico M, Altea T, De Cinti B, Matteucci G (2015) A guild-based
365 approach to assessing the influence of beech forest structure on bird communities. *Forest
366 Ecology and Management* 356:216-223.

367 Batary P, Baldi A (2004) Evidence of an edge effect on avian nest success. *Conservation*
368 *Biology* 18:389-400.

369 Berg Å (1997) Diversity and abundance of birds in relation to forest fragmentation, habitat
370 quality and heterogeneity. *Bird Study* 44:355-366.

371 Böhm SM, Kalko EK (2009) Patterns of resource use in an assemblage of birds in the canopy
372 of a temperate alluvial forest. *Journal of Ornithology* 150:799-814.

373 Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a
374 long-distance migrant bird. *Nature* 411:296-298.

375 Bulluck JF, Rowe MP (2006) The use of southern Appalachian wetlands by breeding birds,
376 with a focus on Neotropical migratory species. *The Wilson Journal of Ornithology* 118:399-
377 410.

378 Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical*
379 *information-theoretic approach*. Springer-Verlag. USA, 515p.

380 Canterbury GE, Martin TE, Petit DR, Petit LJ, Bradford DF (2000) Bird communities and
381 habitat as ecological indicators of forest condition in regional monitoring. *Conservation*
382 *Biology* 14:544-558.

383 Caprio E, Ellena I, Rolando A (2009) Assessing habitat/landscape predictors of bird diversity
384 in managed deciduous forests: a seasonal and guild-based approach. *Biodiversity and*
385 *conservation* 18:1287-1303.

386 Castaño-Villa GJ, Ramos-Valencia SA, Fontúrbel FE (2014) Fine-scale habitat structure
387 complexity determines insectivorous bird diversity in a tropical forest. *Acta Oecologica*
388 61:19-23.

389 Chen J, Chen Z (2008) Extended Bayesian information criteria for model selection with large
390 model spaces. *Biometrika* 95:759-771.

391 Chessel D, Thioulouse J, Dray S (2003) Co-inertia analysis and the linking of ecological data
392 tables. *Ecology* 84:3078-3089.

393 Cody ML (1981) Habitat selection in birds: the roles of vegetation structure, competitors, and
394 productivity. *BioScience* 31:107-113.

395 Deng WH, Gao W (2005) Edge effects on nesting success of cavity-nesting birds in
396 fragmented forests. *Biological Conservation* 126:363-370.

397 Devictor V, Godet L, Julliard R, Couvet D, Jiguet F (2007) Can common species benefit from
398 protected areas? *Biological Conservation* 139:29-36.

399 Donovan TM, Jones PW, Annand EM, Thompson FR (1997) Variation in local-scale edge
400 effects: mechanisms and landscape context. *Ecology* 78:2064-2075.

401 Dubois PJ, Le Maréchal P, Oliosio G, Yésou P (2008) *Nouvel inventaire des oiseaux de*
402 *France*. Delachaux et Niestlé. Slovenia, 559p.

403 Estades CF, Temple SA (1999) Deciduous-forest bird communities in a fragmented landscape
404 dominated by exotic pine plantations. *Ecological Applications* 9:573-585.

405 Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. *The*
406 *American Naturalist* 153:165-182.

407 Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction.
408 *The Journal of Wildlife Management* 61:603-610.

409 Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology,*
410 *Evolution, and Systematics* 64:487-515.

411 Flather CH, Sauer JR (1996) Using landscape ecology to test hypotheses about large-scale
412 abundance patterns in migratory birds. *Ecology* 77:28-35.

413 Freemark KE, Merriam HG (1986) Importance of area and habitat heterogeneity to bird
414 assemblages in temperate forest fragments. *Biological Conservation* 36:115-141.

415 Gates JE, Giffen NR (1991) Neotropical migrant birds and edge effects at a forest-stream
416 ecotone. *Wilson Bulletin* 103:204-217.

417 Gelman A, Hill J (2007) Data analysis using regression and multilevel hierarchical models.
418 New Cambridge University Press. York, NY, USA, 625p.

419 Gharehaghaji M, Shabani AA, Feghhi J, Danekar A, Kaboli M, Ashrafi S (2012) Effects of
420 landscape context on bird species abundance of tree fall gaps in a temperate deciduous forest
421 of Northern Iran. *Forest Ecology and Management* 267:182-189.

422 Goetz SJ, Steinberg D, Dubayah R, Blair B (2007). Laser remote sensing of canopy habitat
423 heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA.
424 *Remote Sensing of Environment* 108:254-263.

425 Goetz SJ, Steinberg D, Betts MG, Holmes RT, Doran PJ, Dubayah R, Hofton M (2010) Lidar
426 remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology*
427 91:1569-1576.

428 Goldstein MI, Corson MS, Lacher Jr TE, Grant WE (2003) Managed forests and migratory
429 bird populations: evaluating spatial configurations through simulation. *Ecological Modelling*
430 162:155-175.

431 Gregory RD, Vorisek P, Van Strien A, Gmelig Meyling AW, Jiguet F, Fornasari L, Reif J,
432 Chylarecki P, Burfield IJ (2007) Population trends of widespread woodland birds in Europe.
433 *Ibis* 149:78-97.

434 Griffis-Kyle KL, Beier P (2005) Migratory strategy and seasonal patterns of bird diversity in
435 relation to forest habitat. *The American Midland Naturalist* 153:436-443.

436 Groupe ornithologique breton (2012). Atlas des oiseaux nicheurs de Bretagne. Delachaux et
437 Niestlé. France, 512p.

438 Grytnes JA, Vetaas OR (2002) Species richness and altitude: a comparison between null
439 models and interpolated plant species richness along the Himalayan altitudinal gradient,
440 Nepal. *The American Naturalist* 159:294-304.

441 Hansbauer MM, Storch I, Knauer F, Pilz S, Küchenhoff H, Végvári Z, Pimentel RG, Metzger
442 JP (2010) Landscape perception by forest understory birds in the Atlantic Rainforest: black-
443 and-white versus shades of grey. *Landscape Ecology* 25:407-417.

444 Herkert JR (1994) The effects of habitat fragmentation on midwestern grassland bird
445 communities. *Ecological Applications* 4:461-471.

446 Holmes RT, Sherry TW, Sturges FW (1986) Bird community dynamics in a temperate
447 deciduous forest: long-term trends at Hubbard Brook. *Ecological Monographs* 56:201-220.

448 Isotti R, Battisti C, Luiselli L (2015) Seasonal and habitat-related changes in bird assemblage
449 structure: applying a diversity/dominance approach to Mediterranean forests and wetlands.
450 *Israel Journal of Ecology & Evolution* 61:28-36.

451 James FC, Wamer NO (1982) Relationships between temperate forest bird communities and
452 vegetation structure. *Ecology* 63:159-171.

453 Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in
454 long–distance migrants, delays in short–distance migrants. *Proceedings of the Royal Society*
455 *of London Series B: Biological Sciences* 270:1467-1471.

456 Jiguet F, Devictor V, Julliard R, Couvet D, Lee A (2007) Functional homogenization effect of
457 urbanization on bird communities. *Conservation Biology* 21:741-751.

458 Julliard R, Jiguet F, Couvet D (2003) Common birds facing global changes: what makes a
459 species at risk? *Global Change Biology* 10:148-154

460 Keller GS, Ross BD, Klute DS, Yahner RH (2009) Temporal changes in migratory bird use of
461 edges during spring and fall seasons in Pennsylvania. *Northeastern Naturalist* 16:535-552.

462 Korňan M, Holmes RT, Recher HF, Adamik P, Kropil R (2013) Convergence in foraging
463 guild structure of forest breeding bird assemblages across three continents is related to habitat
464 structure and foraging opportunities. *Community Ecology* 14:89–100.

465 Kroodsma RL (1984). Effect of edge on breeding forest bird species. *The Wilson Bulletin*
466 96:426-436.

467 Lindenmayer DB, Fischer J (2013) *Habitat fragmentation and landscape change: an*
468 *ecological and conservation synthesis*. Island Press. England, 352p.

469 Loiselle BA, Blake JG (1991) Temporal variation in birds and fruits along an elevational
470 gradient in Costa Rica. *Ecology* 72:180-193.

471 Ludwig M, Schlinkert H, Holzschuh A, Fischer C, Scherber C, Trnka A, Tschardt T, Batary
472 P (2012) Landscape-moderated bird nest predation in hedges and forest edges. *Acta*
473 *Oecologica* 45:50-56.

474 Luoto M, Virkkala R, Heikkinen RK, Rainio K (2004) Predicting bird species richness using
475 remote sensing in boreal agricultural-forest mosaics. *Ecological Applications* 14:1946-1962.

476 Lynch JF, Whigham DF (1984) Effects of forest fragmentation on breeding bird communities
477 in Maryland, USA. *Biological Conservation* 28:287-324.

478 Martinez-Morales MA (2005) Landscape patterns influencing bird assemblages in a
479 fragmented Neotropical cloud forest. *Biological Conservation* 121:117-126.

480 McCollin D (1998) Forest edges and habitat selection in birds: a functional approach.
481 *Ecography* 21:247-260.

482 McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: Spatial Pattern Analysis
483 Program for Categorical and Continuous Maps. Computer software program produced by the
484 authors at the University of Massachusetts, Amherst.

485 Mönkkönen M, Helle P, Soppela K (1990) Numerical and behavioural responses of migrant
486 passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction
487 in northern breeding bird communities? *Oecologia* 85:218-225.

488 Murcia C (1995) Edge effects in fragmented forests: implications for conservation. *Trends in*
489 *Ecology & Evolution* 10:58-62.

490 Naoe S, Sakai S, Sawa A, Masaki T (2011) Seasonal difference in the effects of fragmentation
491 on seed dispersal by birds in Japanese temperate forests. *Ecological Research* 26:301-309.

492 Patterson MP, Best LB (1996) Bird abundance and nesting success in Iowa CRP fields: The
493 importance of vegetation structure and composition. *American Midland Naturalist* 135:153-
494 167.

495 Penhollow ME, Stauffer F (2000) Large-scale habitat relationships of Neotropical migratory
496 birds in Virginia. *The Journal of Wildlife Management* 64:362-373.

497 Petit DR, Petit KE, Grubb Jr TC (1985) On atmospheric moisture as a factor influencing
498 distribution of breeding birds in temperate deciduous forest. *The Wilson Bulletin* 97:88-96.

499 Poulsen BO (2002) Avian richness and abundance in temperate Danish forests: tree variables
500 important to birds and their conservation. *Biodiversity and Conservation* 11:1551-1566.

501 Proença VM, Pereira HM, Guilherme J, Vicente L (2010) Plant and bird diversity in natural
502 forests and in native and exotic plantations in NW Portugal. *Acta Oecologica* 36:219-226.

503 R Development Core Team (2016) R: A language and environment for statistical computing.
504 R Foundation for Statistical Computing. Vienna, Austria.

505 Ralph CJ, Droege S, Sauer JR (1995) Managing and monitoring birds using point counts:
506 standards and applications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149 161-168.

507 Raymond CM, Fazey I, Reed MS, Stringer LC, Robinson GM, Evely AC (2010) Integrating
508 local and scientific knowledge for environmental management. *Journal of environmental*
509 *management*, 91:1766-1777.

510 Renner SC, Gossner MM, Kahl T, Kalko EK, Weisser WW, Fischer M, Allan E (2014)
511 Temporal changes in randomness of bird communities across Central Europe. *PLoS One* 9
512 doi:10.1371/journal.pone.0112347.

513 Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian
514 Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications
515 for conservation. *Biological Conservation* 142:1141-1153.

516 Ries L, Sisk TD (2004) A predictive model of edge effects. *Ecology* 85:2917-2926.

517 Robinson SK, Thompson RF, Donovan MT, Whitehead DR, Faaborg J (1995) Regional forest
518 fragmentation and the nesting success of migratory birds. *Science* 267:93-102.

519 Rodewald AD (2002) Nest predation in forested regions: landscape and edge effects. *The*
520 *Journal of Wildlife Management* 66:634-640.

521 Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, Van Bommel FP (2006) Long-term
522 population declines in Afro-Palearctic migrant birds. *Biological Conservation* 131:93-105.

523 Thomson RL, Forsman JT, Mönkkönen M (2003) Positive interactions between migrant and
524 resident birds: testing the heterospecific attraction hypothesis. *Oecologia* 134:431-438.

525 Tryjanowski P, Kuźniak S, Sparks TH (2005) What affects the magnitude of change in first
526 arrival dates of migrant birds? *Journal of Ornithology* 146:200-205.

527 Vetter D, Rucker G, Storch I (2013) A meta-analysis of tropical edge effects on bird nest
528 predation risk: edge effect in avian nest predation. *Biological Conservation* 159:382-395.

529 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and*
530 *extensions in ecology with R*. Springer. USA, 574p.

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542 **TABLES**

543 **Table 1.** Environmental variables influenced bird community indicators. Summary of the best
 544 mixed models explaining each indicator of bird community by environmental variables. The
 545 effect of each significant fixed variables is indicated with its standardized regression
 546 coefficient and significance (*: P<0.05; **: P<0.01; ***: P<0.001) and the random effect is
 547 also indicated when significant (see Methods for model construction). N is the whole sample
 548 size and Adj-R² is the adjusted R-squared. Diversity is evaluated by the Shannon index.

Bird community indicator	Effect of environmental variables							Random effect (month)		N	Adj-R ²
	distance to edge	coniferous	deciduous	elevation	heterogeneity	basal area	coppice	Inter:	Intra:		
								lower/estimate/ upper	lower/estimate/ upper		
<i>Abundance</i>	-0.30*		0.32*					0.1/0.4/1.2	0.8/0.9/1.1	87	0.21
<i>Diversity</i>	-0.38**		0.36**							87	0.12
<i>Evenness</i>				-0.23*						87	0.05
<i>Residents</i>				-0.42***				0.1/0.3/1.1	0.7/0.9/1.0	87	0.27
<i>Short-distance migrants</i>	-0.46***									87	0.26
<i>Long-distance migrants</i>				0.32***				0.2/0.6/1.8	0.7/0.8/0.9	87	0.45

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560 **Table 2.** Relationships between environmental variables and short-distance migrants persisted
561 along the breeding season, while relationships between environmental variables and
562 abundances of residents and long-distance migrants changed. Summary of the best multiple
563 linear models explaining abundances of residents, short-distance migrants and long-distance
564 migrants by environmental variables, at the three months of the breeding season. The effect of
565 each significant variables is indicated with its standardized regression coefficient and
566 significance (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). Other model parameters are the degree of
567 freedom (Df), the F statistic (F), the P -value (P), and the adjusted R-squared (Adj-R²).

Abundance of	Month	Effect of environmental variables							Df	F	P	Adj-R ²	
		distance to edge	coniferous	deciduous	elevation	heterogeneity	basal area	coppice					
Residents	April				-0.59***				27	14.6	<0.001	0.33	
	May	-0.37*		0.86***				-0.44*	25	6.7	<0.001	0.38	
	June						0.37*		27	4.2	<0.05	0.10	
Short-distance migrants	April	-0.57**						-0.60**	-0.50*	25	6.0	<0.01	0.35
	May	-0.89**		0.54*		-0.65*		-0.37*		24	3.5	<0.05	0.26
	June	-0.42*						-0.38*	-0.57**	25	3.4	<0.05	0.21
Long-distance migrants	April	0.61*	0.41*			0.70*				25	2.6	<0.05	0.15
	May				0.42*					27	5.9	<0.05	0.15
	June			0.68***	0.30*			-0.43*		25	6.4	<0.001	0.37

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576 **FIGURES CAPTIONS**

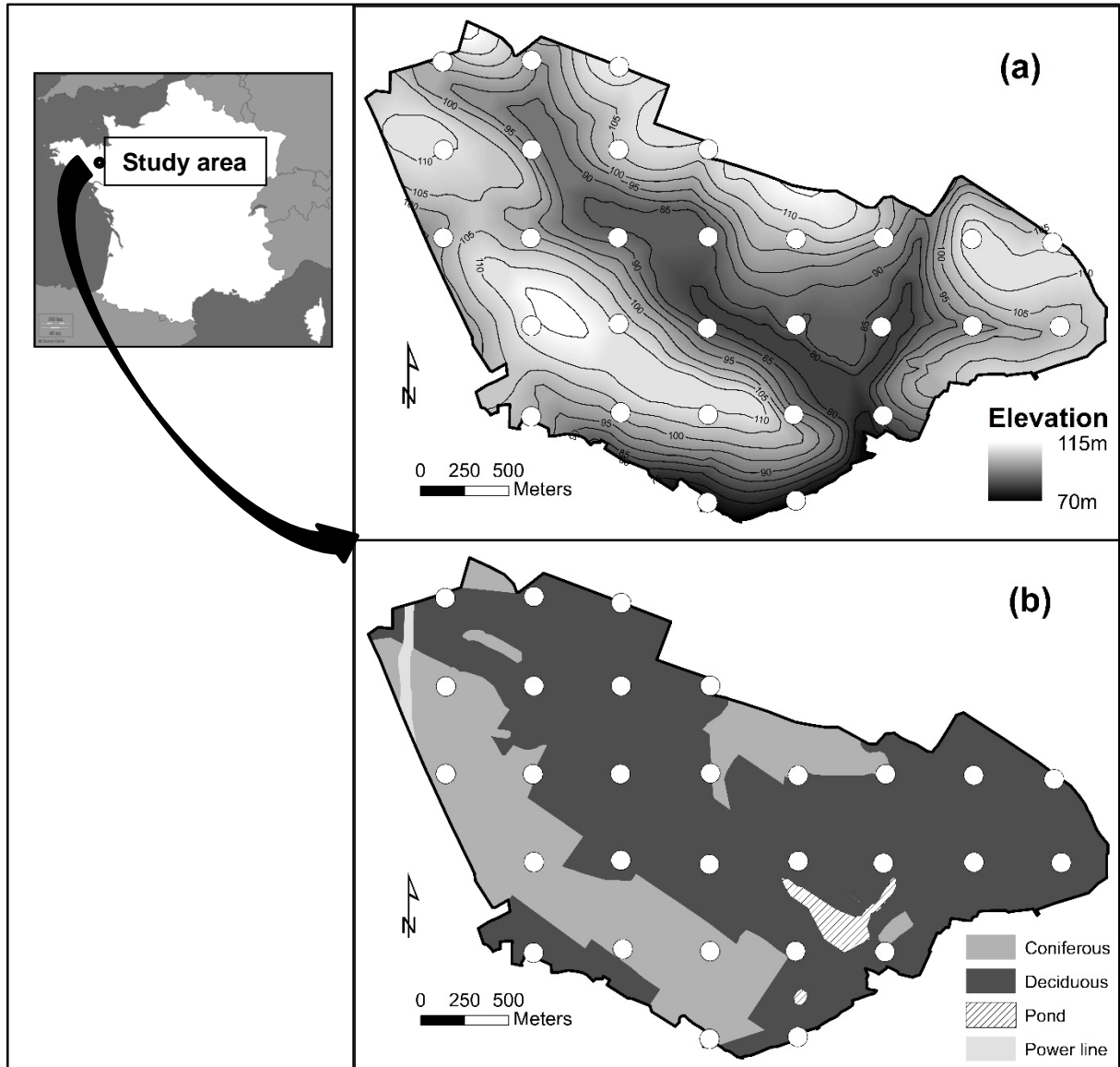
577 **Figure 1.** Localisation of the study area and positions of the 29 bird point counts (500 m
578 square grid), with (a): Elevation data and (b): Areas with dominant deciduous or coniferous
579 tree communities.

580 **Figure 2.** Environmental variables drove individual abundance of bird species. PC1/PC2 co-
581 inertia plane with projection of species (*italics*) and environmental variables (**bold**).
582 Correlation coefficient=0.50, $P=0.001$ and total inertia=61.7%. Species codes: Frco: *Fringilla*
583 *coelebs*; Erru: *Erithacus rubecula*; Trtr: *Troglodytes troglodytes*; Tume: *Turdus merula*; Phco:
584 *Phylloscopus collybita*; Copa: *Columba palumbus*; Syat: *Sylvia atricapilla*; Sieu: *Sitta*
585 *europaea*; Cebr: *Certhia brachydactyla*; Tuph: *Turdus philomelos*; Paca: *Parus caeruleus*;
586 Tuvi: *Turdus viscivorus*; Dema: *Dendrocopos major*; Cocor: *Corvus corone*; Pama: *Parus*
587 *major*; Cuca: *Cuculus canorus*; Oror: *Oriolus oriolus*; Phsi: *Phylloscopus sibilatrix*; Gagl:
588 *Garrulus glandarius*; Papa: *Parus palustris*; Sttu: *Streptopelia turtur*; Rere: *Regulus regulus*;
589 Antr: *Anthus trivialis*; Pivi: *Picus viridis*; Phph: *Phoenicurus phoenicurus*; Sybo: *Sylvia*
590 *borin*; Prmo: *Prunella modularis*; Reig: *Regulus ignicapilla*; Deme: *Dendrocopos medius*;
591 Stvu: *Sturnus vulgaris*; Drma: *Dryocopus martius*; Aeca: *Aegithalos caudatus*; Pacr: *Parus*
592 *cristatus*; Bubu: *Buteo buteo*; Acni: *Accipiter nisus*.

593 **Figure 3.** Influence of elevation on abundance of resident birds (filled triangles and full
594 lines), short-distance migrant birds (empty points and fine-dashed lines) and long-distance
595 migrant birds (filled points and large-dashed lines), over the entire breeding season. See Table
596 1 for models.

597 **Figure 4.** Influence of distance to edge and coppice cover on abundance of resident birds
598 (filled triangles and full lines), short-distance migrant birds (empty points and fine-dashed
599 lines) and long-distance migrant birds (filled points and large-dashed lines), for the three

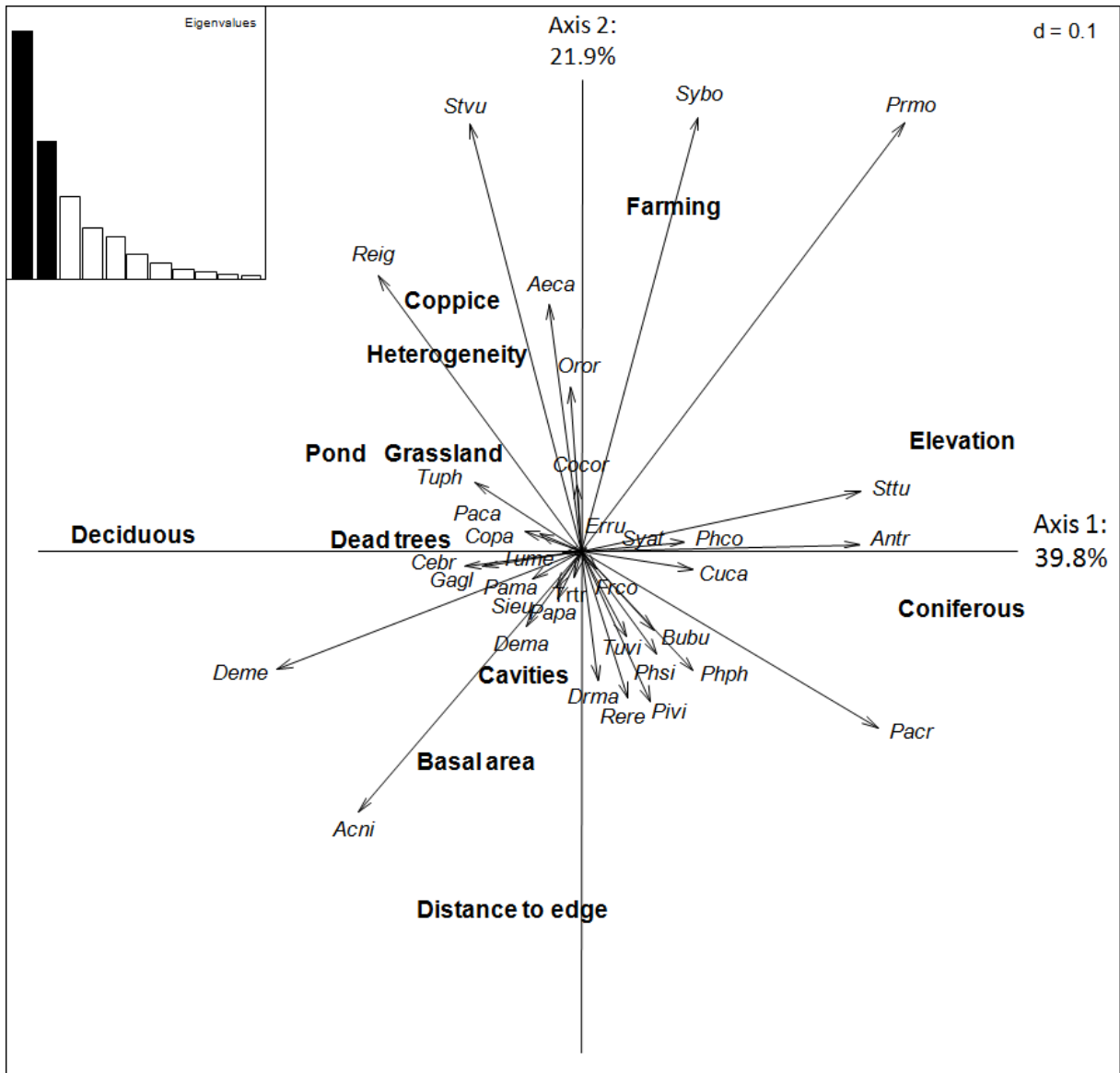
600 months of the breeding season. Both variables are the most frequently significant among
601 relationships between bird abundances and environmental variables at the three months of the
602 breeding season. See Table 2 for models.



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604 **Figure 1.**

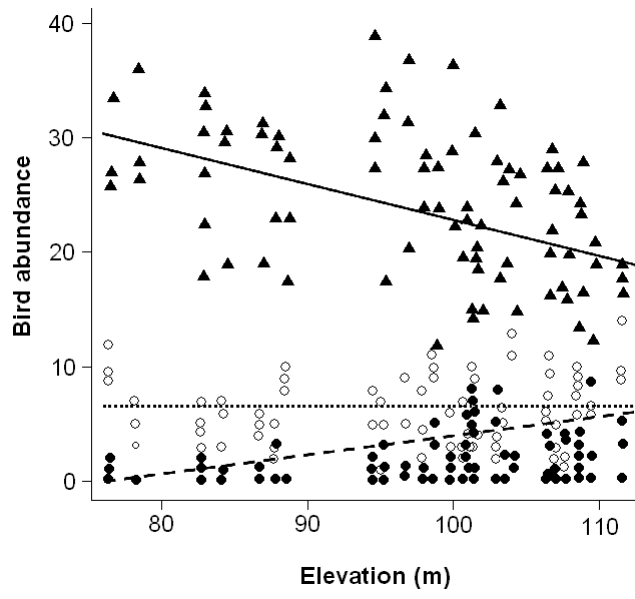
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607 **Figure 2.**

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610 **Figure 3.**

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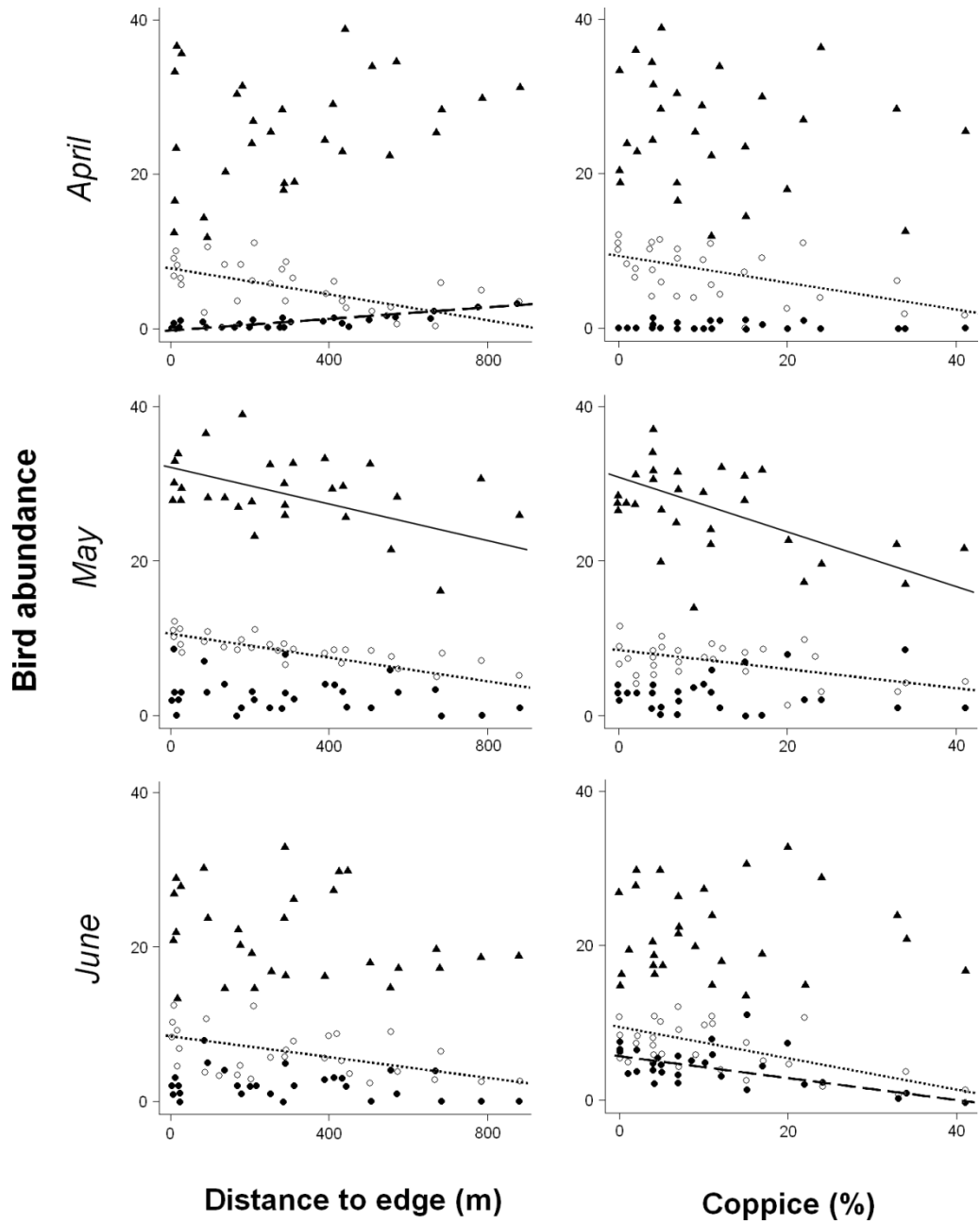
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618 **Figure 4.**

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