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14 **Breeding bird species diversity across gradients of land use from forest to**
15 **agriculture in Europe**

16

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45 **Running title:** Bird species richness and diversity across forest-agricultural land gradients

46 **Key words:** conservation, ecological traits, landscape, management, region, richness, threshold

47

48 **Abstract**

49 Loss, fragmentation and decreasing quality of habitats have been proposed as major threats to
50 biodiversity world-wide, but relatively little is known about biodiversity responses to multiple
51 pressures, particularly at very large spatial scales. We evaluated the relative contributions of
52 four landscape variables (habitat cover, diversity, fragmentation and productivity) in
53 determining different components of avian diversity across Europe. We sampled breeding birds
54 in multiple 1-km² landscapes, from high forest cover to intensive agricultural land, in eight
55 countries during 2001–02. We predicted that the total diversity would peak at intermediate
56 levels of forest cover and fragmentation, and respond positively to increasing habitat diversity
57 and productivity; forest and open-habitat specialists would show threshold conditions along
58 gradients of forest cover and fragmentation, and respond positively to increasing habitat
59 diversity and productivity; resident species would be more strongly impacted by forest cover
60 and fragmentation than migratory species; and generalists and urban species would show weak
61 responses. Measures of total diversity did not peak at intermediate levels of forest cover or
62 fragmentation. Rarefaction-standardized species richness decreased marginally and linearly
63 with increasing forest cover and increased non-linearly with productivity, whereas all measures
64 increased linearly with increasing fragmentation and landscape diversity. Forest and open-
65 habitat specialists responded approximately linearly to forest cover and also weakly to habitat
66 diversity, fragmentation and productivity. Generalists and urban species responded weakly to
67 the landscape variables, but some groups responded non-linearly to productivity and marginally
68 to habitat diversity. Resident species were not consistently more sensitive than migratory
69 species to any of the landscape variables. These findings are relevant to landscapes with
70 relatively long histories of human land-use, and they highlight that habitat loss, fragmentation
71 and habitat-type diversity must all be considered in land-use planning and landscape modeling
72 of avian communities.

73

74 **1. Introduction**

75

76 Declines in biodiversity are occurring in many parts of the world as a result of the degradation,
77 loss and fragmentation of habitat through human activities (e.g., Sodhi and Ehrlich 2010,
78 Newbold et al. 2015). Policy tools to halt this negative trend include, for example, international
79 agreements (such as the European Union's Biodiversity Strategy 2020 and the Convention on

80 Biological Diversity Aichi Biodiversity Targets), establishment of reserves, and legislation on
81 conservation and land use. The full inclusion of these agreements and tools into management,
82 however, requires research on species responses to different forms of anthropogenic land use,
83 such as agriculture or forestry.

84 Human land use affects the amount, spatial configuration, structural heterogeneity and
85 productivity of habitat, and these may all determine biodiversity from the spatial scales of
86 patches to landscapes (see below). By “patches” we refer to relatively uniform areas of a given
87 habitat type and successional stage of vegetation, up to a few hectares in size. By “landscapes”,
88 on the other hand, we refer to areas that consist of multiple patches and are at least several
89 tens of hectares in size. The negative effect of habitat loss is predicted by the classical theory of
90 the species-area relationship (Schoener 1976), which is supported by abundant empirical
91 evidence (Fahrig 2003). At a general level, this relationship is widely accepted, but sometimes
92 habitat loss has impacted biodiversity non-linearly, characterized by threshold responses (e.g.,
93 Huggett 2005). These thresholds have commonly been reported at about 10–30% habitat cover
94 (Swift and Hannon 2010), but they vary notably. For example, Betts et al. (2010) found species-
95 specific canopy-cover thresholds to occur between 1.4% and 24.6%, below which bird
96 occurrence declined markedly. Other studies suggest higher thresholds: Estavillo et al. (2013)
97 studied landscapes with varying degrees of forest fragmentation and detected an abrupt
98 decline in species richness of closed-forest mammals at or below 30% forest cover, and
99 Martensen et al. (2012) found a threshold of drastic avian richness decrease at 30–50% cover in
100 Atlantic forests of Brazil. However, not all studies have reported such thresholds (e.g., Villard et
101 al. 1999, Mikusiński and Angelstam 2004).

102 Thresholds suggest that habitat loss alone may not be responsible for changes in the
103 abundance and occurrence of species. The spatial configuration of habitat – commonly referred
104 to as fragmentation, which includes the division of formerly contiguous habitat and increases in
105 inter-patch distances – may also play a role, particularly if the amount of habitat subject to
106 fragmentation is small (Andrén 1994). The logic underlying the negative impact of
107 fragmentation lies in the idea that the persistence of patchy populations requires dispersal
108 between habitat patches (Hanski 2005). Even for relatively well-dispersing taxa, such as many
109 birds, movements between patches become increasingly difficult with increasing fragmentation
110 (Enoksson et al. 1995, Swift and Hannon 2010). A commonly accepted view is that habitat loss
111 and fragmentation act in concert, and their effects are therefore difficult to distinguish in real-
112 life situations (e.g., Fahrig 2003, 2017, Didham et al. 2012). Indeed, McGarigal and McComb
113 (1995), Trzcinski et al. (1999) and Villard et al. (1999) showed that both forest cover and
114 configuration were good predictors of the occupancy and abundance of breeding forest birds.

115 The niche theory (Hutchinson 1957) provides yet another explanation for variation in
116 biodiversity. Increasing structural heterogeneity potentially reflects a greater variety of
117 habitats, i.e. more niches, which in turn may allow more species to occur in the same general
118 area. Many studies have confirmed the positive link between habitat heterogeneity and species

119 diversity (e.g., Raivio and Haila 1990, Böhning-Gaese 1997, Pino et al. 2000, Luoto et al. 2004,
120 Gil-Tena et al. 2007). Accordingly, loss of structural heterogeneity has led to drastic declines of
121 biodiversity in both agricultural (Benton et al. 2003) and forested landscapes (Gauthier et al.
122 2015).

123 Biodiversity may also be positively associated with productivity (Tilman 1980, 1999). Solar
124 energy and water availability limit plant biomass and diversity, and they, in turn, will determine
125 herbivore and, subsequently, predator biomass and diversity (Huston 1994). This productivity-
126 richness relationship may be hump-shaped (Ricklefs and Schluter 1993). However, many studies
127 have reported linear relationships, but these discrepancies may result from variation in spatial
128 scale among studies (Chase and Leibold 2002). Thus, at a local scale, a hump-shaped curve may
129 be expected, whereas across landscapes or regions, a linear response may be more common
130 (Chase and Leibold 2002). This is because, at landscape or regional scales, species compositions
131 tend to become increasingly different between patches with increasing productivity.

132 Species traits determine biological responses to environmental variation and change. For
133 instance, habitat specialists may be more severely impacted than generalists by loss and
134 fragmentation of habitat (Schmiegelow and Mönkkönen 2002, Virkkala and Rajasärkkä 2006;
135 but see Fahrig 2017), the latter being expected to be more adaptable to a range of conditions,
136 including anthropogenic impacts. Similarly, urban species tend to be generalists in terms of
137 niche position, though urban communities are typically comprised of species from a range of
138 natural habitat types (Evans et al. 2010). Furthermore, resident species may be more sensitive
139 than migratory species in this respect (Enoksson et al. 1995, Roberge and Angelstam 2006). This
140 is because the movements of resident species are often more constrained than those of
141 migratory species (Desrochers et al. 1999).

142 The majority of biological evidence that guides current land use is based on experiments or *ad*
143 *hoc* comparisons conducted between patches of habitat rather than at the landscape level (cf.
144 Koivula et al. 2014). The latter types of studies are urgently needed because certain biological
145 phenomena cannot be fully explored at the patch level. These include responses of species
146 assemblages that usually change gradually between patches of different habitat types, land-use
147 impacts on species with home ranges covering multiple patches of sometimes different site
148 types, or responses of species to landscape-level habitat use.

149 One approach to understanding implications of landscape changes is to examine biological
150 communities across gradients of land use (e.g., Matson 1990, McDonnell and Pickett 1990, Blair
151 1996, 1999, O'Connell et al. 2000, Coppedge et al. 2001, Ribera et al. 2001, Sousa et al. 2004,
152 Vanbergen et al. 2005). If constructed in a consistent manner, gradients can provide insights
153 into the generality of responses of communities to environmental change. Such an approach is
154 used in this paper to assess how the richness and diversity of breeding birds vary across
155 gradients of land use in eight European countries. These gradients represent shifts from
156 continuous forest at one extreme, through mosaics of forest and agricultural land, to a
157 dominance of agricultural land at the other extreme. Such complete gradients of habitat cover

158 have commonly produced intermediate richness peaks in abundance and richness of birds
159 (Jokimäki and Suhonen 1993, Andrén 1994, Cushman and McGarigal 2003, Desrochers et al.
160 2011).

161 In the present paper, we attempt to identify the key landscape variables that drive bird species
162 richness and diversity across gradients of forest cover using a unique data set based on
163 standardized sampling methods over a large geographic area, from boreal to Mediterranean
164 regions. More specifically, we present an analysis of the relative contributions of cover and
165 fragmentation of forests, and structural diversity and productivity of landscapes on the species
166 richness of bird communities. Based on research summarized above, we made the following
167 predictions:

168 1. The total avian diversity (i.e., of all species) should peak at intermediate levels of forest cover
169 and fragmentation, and should be positively associated with increases in habitat diversity and
170 productivity.

171 2. The diversity of forest-associated species should show a threshold for a decline within the
172 range of 10–50% of forest cover (e.g., Swift and Hannon 2010, Martensen et al. 2012), and
173 below this threshold, fragmentation should become increasingly important. This richness
174 measure should also increase with increasing diversity of forests, and productivity.

175 3. The diversity of open-habitat species should decline in the range 50–90% of forest cover
176 (compare prediction #2) and with decreasing forest fragmentation, as – in the present study
177 context – these broadly correspond to higher proportions and continuity of open habitats. The
178 diversity of open-habitat species should also increase with increasing diversity of open habitats,
179 and productivity.

180 4. Resident species should show stronger responses to forest cover and fragmentation than
181 migratory species.

182 5. Species that commonly breed in both forests and open habitats (hereafter “generalists”), or
183 in residential and industrial areas (hereafter “urban species”), should show no strong trends
184 along the gradient.

185

186 **2. Material and methods**

187

188 *2.1. Study design and field methods*

189

190 We conducted the study in eight European countries: Finland, France, Hungary, Ireland,
191 Portugal, Spain, Switzerland and the United Kingdom (UK) (Fig. 1). We selected a total of six

192 sample sites, termed Land-use Units (LUUs), in one region of each of the eight countries. Each
193 LUU consisted of a 1-km² square of differing habitat composition with respect to the relative
194 amounts of forest cover and agricultural land, selected to be representative of the regional land
195 use in each country (Supplementary materials, Table S1).

196 Within each LUU, we located 16 points on a regular 200 m × 200 m grid with the outermost
197 points positioned 200 m from the edge. We collected bird data using point counts (Verner
198 1985) at each of the 16 sampling points per LUU. In each year, we made four counts at each
199 point, each count lasting five minutes. We undertook the four counts as near to dawn as
200 possible on separate occasions (visits) spread throughout the breeding season. In most
201 countries, this was in the months April, May and June, but was slightly earlier in the
202 Mediterranean countries and slightly later in Finland to account for latitudinal variation in the
203 timing of breeding seasons. No counts were undertaken during excessively wet or windy
204 conditions. As far as possible, the counts for individual visits were undertaken at all 16 points
205 within an LUU on the same day. Observers varied the order in which sample points were
206 surveyed on different visits. During each count, the observer recorded all birds seen or heard as
207 long as they were deemed to be using the LUU (e.g., for nesting, displaying, foraging or
208 roosting). The locations of these were recorded within 100-m radius of the point. In this paper,
209 we use records of territorial pairs (indicated by a singing male, observed pair, chicks or nest, or
210 alarm calling individuals) that were noted separately from birds that did not show territorial
211 behavior. We do not believe that double counts of individuals would have biased our data as
212 the sample unit was the LUU, and nearest count stations of adjacent LUUs were at least several
213 hundred meters apart. Our estimations of expected species richness (see below), however,
214 might be somewhat affected by occasional double counts of individuals of loud species within
215 adjacent sampling points.

216 The survey took place over two years, 2001 and 2002. In 2001, due to habitat-identification or
217 access issues, one LUU was not covered in Ireland, Portugal and Spain. In 2002, six LUUs were
218 covered in each country. However, one of our landscape variables – the number of forest
219 patches (see below) – included one Swiss LUU as an outlier (15, while others varied between 0
220 and 8) so samples for both years from this LUU were excluded from analysis.

221

222 *2.2. Data preparation*

223

224 We first determined the maximum number of pairs – recorded within 100 m from the observer
225 – per point across the four visits per year. This is a common way of extracting data based on
226 breeding observations that ensures that all likely breeders are counted (e.g., Sutherland 1996).
227 After this phase, we pooled the 16 points for each LUU, thus resulting in 91 samples (2 years × 8
228 countries × 6 LUUs – 5 LUUs; see above). We then calculated two measures of bird diversity
229 from these data: observed species richness (S_{obs}) and the expected number of species at given

230 levels of abundance (S_{exp}), estimated from rarefaction, which we used to control for the
231 potential greater likelihood of higher species richness occurring purely due to a greater number
232 of individuals (James and Rathbun 1981). We calculated rarefaction separately for abundance
233 levels of 20 and 50 individuals. Samples with fewer than 20 or 50 individuals, respectively, were
234 excluded from these analyses.

235 To evaluate if species traits contributed to forest-cover responses of the bird community, we
236 divided the observed bird species into eight groups based on Cramp et al. (1977-1994), and
237 national expertise and sources (Sharrock 1987, Yeatman-Berthelot and Jarry 1995, Schmid et al.
238 1998, Väisänen et al. 1998, Szep et al. 2012, de Juana and Garcia 2015) (Appendix; see also
239 Acknowledgements). For each group, we calculated S_{obs} for each LUU; due to the lower
240 abundances, sample sizes were much reduced when considering species groups, and therefore
241 S_{exp} was not analyzed. The grouping was based on a combination of migration strategy (resident
242 or migratory), main breeding habitat (forested, open, general) and common occurrence in
243 urban environments. We considered partial migrants – such as the Goldcrest (*Regulus regulus*)
244 in Finland – migratory. Forested habitats included all forest types and their successional stages,
245 and open habitats included dry bushy areas, meadows, pastures, and other types of agricultural
246 land. We considered a given species urban if it commonly occupies industrial and residential
247 areas; wooded city parks were not included. Species associated with wetlands were not
248 common in the data and were therefore not considered. As these species traits varied among
249 the eight countries for a given species, the classification varied accordingly. For example, the
250 Stock Dove (*Columba oenas*) fell into resident species in the Spanish subset, but was considered
251 migratory in that of Finland. Moreover, regarding the habitat criterion, a given species could fall
252 into two categories, e.g., the Wood Pigeon (*Columba palumbus*) was often included in both
253 urban and forest-associated species.

254 As explanatory variables for avian diversity, we used six landscape variables calculated from
255 fused Landsat 7 ETM and IRS images with a 5-m resolution using FRAGSTATS version 3
256 (McGarigal et al. 2002; Supplementary materials, Table S1). For a detailed description of these
257 data, see Watt et al. (2003). These variables were (1) forest cover (%); (2) forest diversity
258 (Shannon-Wiener index based on % covers of forest-habitat types as distinguished in satellite
259 images, including four types of each of broad-leaved, coniferous or mixed forest: recently
260 cleared, very open, open and closed tree canopy); (3) open-habitat diversity (Shannon-Wiener
261 index based on % covers of types of moor, farmland, pasture and meadow as distinguished in
262 satellite images); (4) landscape diversity (Shannon-Wiener index based on % covers of all
263 habitat types as distinguished in satellite images); (5) number of forest patches (n/km^2) as a
264 measure of fragmentation; and (6) Normalized Difference Vegetation Index (NDVI; for a review
265 see Pettorelli et al. 2011) as a surrogate of productivity. These were derived for the 1- km^2 area
266 of each LUU, and they did not strongly correlate with each other (Spearman $\rho < |0.6|$).

267 Fragmentation can be measured in several ways (Fahrig 2003). We used the number of forest
268 patches that reflects the breaking apart of forests, but ignores distances between patches. We

269 also considered all other fragmentation measures provided by FRAGSTATS, but these either
270 correlated strongly with forest cover, landscape/forest/open-habitat diversity or NDVI ($\rho >$
271 $|0.6|$) or their distributions were highly skewed (skewness value $> |3|$).

272

273 *2.3 Statistical analyses*

274 To explain bird diversity patterns across the forest-agricultural land gradients, we used
275 generalized additive models (GAM; cf. Zuur et al. 2009) with regression splines (Wood 2003).
276 We ran the GAMs using year (2001 or 2002, to account for temporal dependence of samples)
277 and country (the eight countries, to account for spatial dependence of measures on geographic
278 variation) as random effects, and the six landscape variables (see above) as continuous fixed
279 effects, subject to smoothing. Each model included only prediction-based subsets of the six
280 landscape variables (see below). Prior to the analysis, we scaled all landscape variables to vary
281 between 0 and 100. We did not include interaction terms due to the low numbers of repeated
282 measures (two years) and spatial replication (six samples per country), and the ambiguity of the
283 interpretation of smoother interactions. To avoid over-fitting we set the maximum degrees of
284 freedom for each smooth term to 3, and gamma to 1.4 (Zuur et al. 2009). Regarding the two
285 groups of open-habitat species, however, preliminary runs suggested over-fitting of open-
286 habitat diversity, as the response curve was an S lying on its side (peak-low-peak-low).
287 Therefore, we set the maximum $df = 2$ for open-habitat diversity in these two models. After
288 each preliminary run, we tested the normality of residuals using Q-Q plots (e.g., Sokal and Rohlf
289 1995). The residuals followed a normal distribution in all cases. Hence we applied the Gaussian
290 error distribution with identity link function for the non-integer S_{exp} , but applied the Poisson
291 error distribution with log link function for S_{obs} as it bounds these measures to zero. After each
292 run, we applied Moran's I (Moran 1950) based on model residuals and a latitude-longitude
293 distance matrix to detect possible remaining spatial autocorrelation. There was evidence of
294 significant negative spatial autocorrelation in the whole community measures (S_{obs} , S_{exp20} and
295 S_{exp50}), although this was largely driven by outliers in the Portuguese data set (Supplementary
296 materials, Table S2, Fig. S1). There was no longer significant autocorrelation when this country
297 was omitted and models re-run. Furthermore, results were very similar to the full data set
298 when omitting Portugal (Supplementary materials, Table S3). We therefore conclude that our
299 model outputs were robust to spatial autocorrelation effects.

300 We used the following sets of landscape variables, which were linked respectively to each set of
301 predictions:

302 S_{obs} , S_{exp20} and S_{exp50} = forest cover + forest fragmentation + landscape diversity + NDVI

303 Forest species richness = forest cover + forest fragmentation+ forest diversity + NDVI

304 Open-habitat species richness = forest cover + forest fragmentation + open-habitat diversity +
305 NDVI

306 Generalist and urban species richness = forest cover + forest fragmentation + landscape
307 diversity + NDVI

308 We performed all calculations and analyses using R 3.4.1 (R Core Team 2017) software with
309 mgcv 1.8 (Wood 2017) and ape 4.1 (Paradis et al. 2017) packages. We report % deviance as an
310 indicator of explained variation by each model variable, and adjusted R^2 for the coefficient of
311 determination of the full model. We considered $p \leq 0.05$ significant, but we also note results at
312 $p < 0.10$, which we consider marginally significant.

313

314 **3. Results**

315

316 *3.1. Overall responses to the forest-agricultural land gradients*

317

318 For the three measures of total avian diversity, variation between years did not explain any of
319 the model deviance, whereas variation among the eight countries accounted for on average
320 40.9% (Table 1). The effect of forest cover was small, but marginally significant and negative for
321 both S_{exp} measures, and the effect of number of forest patches – our surrogate for increasing
322 fragmentation of forests – was positive and linear for all three measures, though only
323 marginally so for $S_{\text{exp}20}$ (Table 1). All three total diversity measures positively and linearly
324 responded to increasing landscape diversity. Of the three measures, S_{obs} did not respond to
325 NDVI, but $S_{\text{exp}20}$ and marginally also $S_{\text{exp}50}$ showed approximately concave responses (Table 1,
326 Fig. 2). The S_{exp} measures thus increased rather steeply up to NDVI values of about 0.60–0.70,
327 above which they reached a plateau or even slightly decreased (Table 1, Fig. 2). Due to the
328 similarity of responses among the three measures, only $S_{\text{exp}20}$ is shown in Fig. 2.

329

330 *3.2. Responses of different species-trait groups to the forest-agricultural land gradients*

331

332 For the forest and open-habitat species groups, the variable Year accounted for on average
333 0.3% and Country accounted for on average 27.8% of variation in species richness (Table 2).

334 Forest cover explained on average 9.1% of variation, whereas number of forest patches, forest
335 or open-habitat diversity, and NDVI explained relatively little (averages 1.0%, 1.1% and 1.9%,
336 respectively; Table 2). Forest cover was significant in all cases, its effect resulting in linear or
337 near-linear positive (forest species) or negative responses (open-habitat species) (Fig. 3). The
338 non-linear response of migratory open-habitat species suggests slightly intensifying declines
339 above 30–40% forest cover.

340 Increasing number of forest patches was positively and linearly associated with resident forest
341 species richness, whereas the other three habitat-specialist groups did not respond to this
342 variable (Table 2).

343 Habitat diversity had no detectable effect on forest species or migratory open-habitat species,
344 but resident open-habitat species showed a marginally significant, convex response (Table 2).
345 As such, the curve appears difficult to interpret, and there was no general linear trend along the
346 open-habitat diversity gradient (Spearman correlation for partial residuals: $\rho = -0.17$, $p =$
347 0.103). The partial residuals, however, correlated significantly with open-habitat diversity in
348 LUUs with low, but not in LUUs with high, open-habitat diversity ($\rho = -0.42$ and 0.16 , and $p =$
349 0.006 and 0.269 , respectively).

350 NDVI affected positively and non-linearly – though only marginally – resident forest species,
351 and negatively and linearly both groups of open-habitat species (Table 2, Fig. 4). The former
352 increased rather steeply up to about an index value of 60–70, above which either the richness
353 continued to increase very slowly or reached a plateau (Fig. 4).

354 Generalists showed varying and usually minor responses to the four landscape variables (Table
355 2). Country again accounted for most of the explained variation and Year had virtually no
356 impact. Resident and migratory generalists did not significantly respond to any of the four
357 landscape variables, except to NDVI by resident generalists: their richness increased rather
358 steeply up to a plateau at an index value of about 0.70–0.80 (Fig. 4).

359 The four landscape variables were also generally rather poor predictors of the species richness
360 of urban species (Table 2). Migratory urban species responded positively, albeit only marginally,
361 to increasing landscape diversity, and this group also showed a concave yet marginal response
362 to NDVI, with peak at about 0.60–0.75 (Fig. 4).

363

364 **4. Discussion**

365

366 4.1. Total avian diversity was strongly impacted by country, fragmentation and landscape
367 diversity

368

369 Country was the most important determinant of avian diversity in our data and accounted for,
370 on average, about one-third of explained variation in all 11 analyses. Comparisons between
371 countries were beyond the scope of our analysis, but this striking variation might be explained
372 by, for example, altitudinal variation, land-use history and its current intensity (e.g., Marzluff
373 2001, Eriksson et al. 2002, Vellend 2004), types of forest and farmland, and their associated
374 structural elements (see below). Yet another possibility is solar energy associated with
375 productivity (e.g., Hawkins et al. 2003). Unsurprisingly, country-specific average latitudes of our

376 sampling points correlated negatively with respective growing degree days ($\rho = -0.51$).
377 Growing degree days did not markedly correlate with the total diversity measures, whereas
378 they correlated rather strongly and positively with the species richness of all groups of resident
379 species, and negatively with that of all groups of migratory species (Supplementary materials,
380 Table S4). Thus, large-scale geographic variation, partly linked with solar energy, was notable
381 for all species groups so that migratory species appeared most species rich in the north,
382 whereas resident species showed the opposite tendency.

383 No total diversity measure was markedly affected by forest cover. Thus, our prediction #1 on
384 intermediate diversity peaks along the forest-cover gradient was not supported. Preliminary
385 runs with only year, country and forest cover resulted in rather clear intermediate peaks for the
386 three total diversity measures (Supplementary materials, Table S5, Fig. S2). Different
387 combinations of landscape variables, however, either resulted in a non-significant intermediate
388 peak along the forest-cover gradient, or the trends remained linear, as in Fig. 2. These results
389 suggest that consideration of forest cover alone may give misleading conclusions of its effects
390 on the bird community, and that the apparent decline in diversity at higher levels of forest
391 cover is in fact more closely correlated with other landscape-level variables. Several other
392 factors may thus mediate the effect of forest cover, such as variation in gradient lengths of
393 landscape variables, partial correlations between forest cover and the other landscape
394 variables, or partial correlations between forest cover and unmeasured but important smaller-
395 scale variables, such as habitat structure and land use intensity (see below). Furthermore,
396 although we were interested in general patterns of bird diversity, it should be acknowledged
397 that each country had a unique combination of species, and the responses of individual species
398 in shaping the overall community response between the eight countries is likely to have also
399 been important in causing variability in responses to the gradients considered.

400 All measures of total avian diversity were positively associated with increasing fragmentation
401 and landscape diversity (prediction #1). Similarly, positive relationships between avian richness
402 and landscape structural heterogeneity have earlier been reported by McGarigal and McComb
403 (1995), Böhning-Gaese (1997), Rodewald and Yahner (2002), Tews et al. (2004) and Mitchell et
404 al. (2006). High habitat diversity is a positive feature for biodiversity as long as patches remain
405 sufficiently large for species (Schippers et al. 2015).

406 Our surrogate for productivity (NDVI) had strong effects on expected, but not observed, species
407 richness, the former showing threshold conditions above which the increase rapidly evened out
408 (prediction #1; Fig. 1). At a local level, such as within each of our eight study regions, species
409 richness should peak at intermediate levels of productivity (Chase and Leibold 2002), and the
410 non-linear response of expected richness partly supports this view. The difference between
411 expected (positive response) and observed richness (no response), on the other hand, probably
412 resulted from an increase in abundance of several species along the productivity gradient.

413 A positive association between productivity or energy surrogates and bird richness has earlier
414 been reported for forest specialists in Finnish forest reserves (Honkanen et al. 2010), but to our

415 knowledge, our study is the first to report threshold conditions for species diversity across a
416 productivity gradient. Increasing productivity and resource biomass may result in higher habitat
417 diversity and more trophic levels, which in turn support higher species richness through
418 principles of niche theory (Fretwell 1987, Abrams 1995, Turner et al. 2001, Evans et al. 2006).
419 Above the threshold, productivity continues to increase but the diversity of habitat types and
420 other resources may not do so.

421

422 4.2. Habitat specialists responded strongly to forest cover

423

424 The species richness of forest and open-habitat specialists responded rather linearly to changes
425 in forest cover, providing partial support for our predictions #2-3 (Fig. 3). This linearity could
426 result from bird communities which included a continuity of species with varying home-range
427 or local-population sizes (Haila 2002). Thus, with increasing habitat loss, species requiring large
428 tracts of habitat would disappear first, followed by species with smaller home ranges.
429 Moreover, forest fragmentation, habitat diversity or productivity had generally minor influence,
430 in accord with other studies that have shown that habitat amount is a better predictor of bird
431 abundance or distribution than its spatial configuration (McGarigal and McComb 1995, Trzcinski
432 et al. 1999, Fahrig 2002, 2017). Our results broaden these generalizations to species richness.

433 Regarding the four groups of specialists, we found some support for a forest-cover threshold
434 only for migratory open-habitat species which showed a non-linear relationship (Fig. 3; see also
435 Supplementary materials, Fig. S2). The decline in these specialists began to accelerate at about
436 30–40% forest cover (Fig. 3; see also Supplementary materials, Fig. S2), a value lower than our
437 expected predictions of $\geq 50\%$ forest cover. Moreover, a preliminary analysis with only country,
438 year and forest cover also suggested a threshold in resident forest species richness at about
439 30–50% forest cover (Supplementary materials, Table S5, Fig. S2), in support of our predictions
440 #2-3. Fragmentation may be key for understanding the contrast between this result and that
441 presented in Fig. 3. There was a non-linear relationship between forest cover and the number
442 of forest patches: these variables correlated positively in LUUs with low ($< 50\%$) and negatively
443 in LUUs with high ($\geq 50\%$) forest cover ($\rho = 0.47$ and -0.70 , respectively). Accordingly, the
444 richness of resident forest species correlated clearly with forest cover in low- but less markedly
445 in high-cover samples ($\rho = 0.42$ and 0.21 , respectively), whereas the correlations with patch
446 number were perhaps less prominent, but suggested opposite directions in low- and high-cover
447 samples ($\rho = 0.24$ and -0.26 , respectively). Thus, fragmentation apparently impacted resident
448 forest species when forest cover was low, supporting Andrén (1994) and Hanski (2005).

449 The positive effect of fragmentation on resident forest species supports Fahrig (2017) who
450 showed that most fragmentation responses are positive, even when rare or specialized species
451 are considered. In the present study, this pattern may be partly related to the non-linear
452 covariation between forest cover and number of patches (see above), but also to variation in

453 the degree of specialization. Thus, some of the forest species may be able to tolerate edge
454 conditions in small fragments or even utilize replacement habitats. Different responses to
455 habitat loss by strict habitat specialists and flexible habitat users may result in species turnover
456 (e.g., Schmiegelow et al. 1997). Moreover, if the flexible habitat users increase more rapidly
457 than the rate at which strict specialists disappear, the total richness will increase with
458 increasing fragmentation.

459 Many LUUs with no or very little forest or no agricultural land frequently hosted several species
460 specialized on these habitat categories (Fig. 3). All five LUUs with up to 1% forest cover hosted
461 forest species, the range in richness being 2–9 species. Similarly, among the ten LUUs with at
462 least 99% forest cover, eight hosted open-habitat species (range 1–7 species). Previously, Berg
463 (2002) has shown that many farmland birds can be most abundant in agricultural areas that
464 include forests. These examples suggest flexible habitat use and/or that forest-farmland edges
465 or other minor components of landscapes support these species (e.g., Terraube et al. 2016). It
466 is, therefore, difficult to exactly determine where focal habitat ends and matrix (*sensu* Turner et
467 al. 2001) begins, particularly where species assemblages or communities are concerned. For
468 example, some forest species are able to utilize gardens, rows of trees, or bushy patches
469 (Hinsley and Bellamy 2000, Fuller et al. 2007). Some open-habitat species, on the other hand,
470 utilize forest edges, early stages of secondary succession, or forests with sparsely distributed
471 trees for breeding, foraging or roosting (Berg and Pärt 1994, Reino et al. 2009).

472

473 4.3. Migratory strategy, generalists and urban species, and the effect of productivity

474

475 According to our analysis, migratory strategy was not systematically linked with sensitivity to
476 habitat loss or fragmentation, or any other landscape variable; thus, our prediction #4 was not
477 supported. Responses to forest cover were similar between resident and migratory specialists,
478 and migratory strategy was inconsistently linked with the other landscape variables (Table 2).
479 Such varying responses to landscape structure might be related to the degree of specialization
480 (see above). For example, many closed-forest specialists are also resident, whereas forest-
481 succession generalists are often migratory (Schmiegelow et al. 1997, Schmiegelow and
482 Mönkkönen 2002, Brotons et al. 2003, Virkkala and Rajasärkkä 2006).

483 In line with our prediction #5, generalists and urban species showed rather weak responses
484 and, contrary to specialists (see above), did not respond to forest cover. These patterns may
485 have resulted from these species being rather heterogeneous in terms of requirements for
486 habitat, and/or from being well adapted to changes in land use (e.g., Büchi and Vuilleumier
487 2016). An in-depth understanding of responses to landscape structure by these species would
488 require a species-level approach on abundances or occurrences (Betts et al. 2014), and a
489 multiple-view consideration of specialization. In the present paper, the focus was on species
490 diversity.

491 Two groups of resident species, generalists and forest species, showed threshold conditions
492 along the productivity gradient, following the trend of total richness (Figs. 2 and 4). Migratory
493 urban species, on the other hand, peaked at intermediate productivity, and migratory open-
494 habitat species decreased linearly (Fig. 4). These responses might reflect richness limits set by
495 regional avifauna, but also intensifying intra- or inter-specific interactions, such as resource
496 competition or predation (Fretwell 1987, Abrams 1995). The negative slope of migratory open-
497 habitat species in particular might reflect adaptations to low-competition, resource-poor
498 environments.

499

500 4.4. Structural elements, gradient lengths, spatial scales, and species classifications

501

502 Our set of landscape measures was limited by available satellite images and software. Even
503 where the landscape structure was similar, there could be differences in the quality of habitat
504 (the amount and diversity of structures and processes characteristic of each habitat) for birds
505 within patches that were ostensibly the same. Indeed, several studies have found patch
506 characteristics to be more important than patch area (Benton et al. 2003, Heikkinen et al. 2004,
507 Wretenberg et al. 2010, Galitsky and Lawler 2015, Humphrey et al. 2015). Potentially important
508 factors for avian richness include those that are directly linked to fertility (such as soil type;
509 Mittelbach et al. 2001), land-use intensity (e.g., road length, the amount of traffic, human
510 population density, the proportion of managed and unmanaged habitat; Gnass Giese et al.
511 2015), historical land use, which may be particularly important for poorly-dispersing organisms
512 (Bellemare et al. 2002, De Keersmaeker et al. 2015), and certain structural features of known
513 importance for many specialized species, such as dead wood, very large individual trees, or
514 certain types of micro-habitat that remained undetected in our satellite images (Götmark and
515 Thorell 2003, Luoto et al. 2004).

516 Some effects may also have been missed because of a limited range of variation and “gaps” in
517 our data. Most notably, gradients of landscape diversity and productivity may have represented
518 only part of regional variation, although the landscapes were initially selected so as to be
519 structurally representative for regional forest-agricultural mosaics (Watt et al. 2003). Also, our
520 forest-cover gradient had relatively poor coverage at 25–30% and 60–80%, which may have
521 somewhat impacted our results. Furthermore, larger spatial scales might have produced
522 different results (Stephens et al. 2003). Multi-species studies are also sensitive to at least the
523 selection of species traits to study, and the categorization of species. We attempted to account
524 for the latter issue by applying country specificity in classifying species according to their
525 breeding habitat and migratory strategy, but our approach was nevertheless a simplification.
526 The degree of specialization to habitat conditions by the studied species (Appendix) is rather a
527 gradient than a series of sharply-delimited categories – urban, forest or agricultural land –
528 which may appear important in evaluations of species turnover and associated variation in

529 responses to fragmentation. The regional species pool might have constrained such responses:
530 the number of resident forest species, for example, was 4–8 in Finnish LUUs but was 0–4 in
531 Hungarian LUUs. Our classification also involves subjectivity, although we used both national
532 expertise and inventory-based literature for this (see Material and methods). Different
533 classifications would possibly have resulted in somewhat different results, particularly if more
534 detailed habitat associations were involved (Fuller 2012). However, increasing detail results in
535 lower generality and frequently also sample sizes too low for analysis.

536

537 4.5. Conclusions

538

539 Landscape features determining different diversity measures of the Pan-European bird
540 community were different from those determining the species richness of different ecological
541 groups of birds. The former were consistently determined by the spatial configuration of
542 forests, landscape diversity and often also by productivity, whereas species specialized to
543 forests and open habitats were all determined by forest cover. Generalists and urban species,
544 on the other hand, responded rather weakly to our landscape measures. These results indicate
545 that the amount, fragmentation and structural heterogeneity of habitats, and landscape
546 productivity, all appear important determinants of avian community structure in the sense of
547 species of different habitat preferences and migratory strategies. These thus affect different
548 parts of the bird community in different ways, so no single measure of landscape structure can
549 be used to predict the whole bird community. It must also be emphasized that habitat loss and
550 fragmentation are closely related (Fahrig 2003, 2017, Didham et al. 2012, Villard and Metzger
551 2014). Therefore, both need to be considered in, for example, landscape modeling and
552 conservation planning. The present results also strongly indicate that these two do not suffice,
553 but habitats should in addition be of good quality in terms of habitat-type diversity.

554 Historical, economic and climatic factors complicate the identification of landscape gradients
555 that are exactly the same in different parts of Europe. The relative importance of different
556 structural features may vary accordingly, and processes operating at landscape scales are
557 expected to vary regionally according to landscape history and processes related to interspecific
558 interactions. Moreover, as our analyses showed, bird communities vary structurally among
559 countries, which likely affects their ability to adapt to climatic alterations, habitat loss,
560 fragmentation and altered quality of habitat.

561 A gradient that more accurately reflects anthropogenic disturbance would need to sample
562 pristine habitats. The inclusion of such sites might reveal different results to those described in
563 this paper (cf. Zlonis and Niemi 2014). However, with a few exceptions, such habitats are rare in
564 Europe (Aksenov et al. 1999), so the patterns described here can be considered relevant to the
565 highly disturbed cultural landscapes that dominate most of the continent.

566

567

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576

577

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801

802

803 Figure legends

804

805 **Fig. 1.** The locations of eight study countries: Finland (FIN), France (FRA), Hungary (HUN),
806 Ireland (IRE), Portugal (POR), Spain (ESP), Switzerland (SWZ) and the United Kingdom (UK).

807 Source for the basic map:

808 https://commons.wikimedia.org/wiki/File:Europe_laea_location_map.svg; used under the
809 Creative Commons license CC-BY-SA-3.0. Adapted from the original map by slightly cropping,
810 and by adding country points and abbreviations.

811

812 **Fig. 2.** GAM plots for the expected species richness for 20 individuals (S_{exp20}). For descriptions of
813 model variables, see Material and methods; for statistical significance, see Table 1. Residuals
814 for each country are shown with different colors (see legend box); solid line shows a curve
815 predicted by the model; dash lines show standard error intervals for the curve.

816

817 **Fig. 3.** GAM plots for resident and migratory forest and open-habitat species against forest
818 cover. For other model variables and statistical significance, see Table 2. Residuals for each
819 country are shown with different colors (see legend box); solid line shows a curve predicted by
820 the model; dash lines show standard error intervals for the curve.

821

822 **Fig. 4.** GAM plots for four groups of species showing significant or marginally significant
823 responses to Normalized Difference Vegetation Index (NDVI). For other model variables and
824 statistical significance, see Table 2. Residuals for each country are shown with different colors
825 (see legend box); solid line shows a curve predicted by the model; dash lines show standard
826 error intervals for the curve.

827

828 **Table 1.** GAM results for different measures of total avian diversity: observed species richness (S_{obs}) and
 829 expected richness for 20 and 50 individuals (S_{exp20} and S_{exp50} , respectively). For explanatory variables, see
 830 Material and methods; Dev% = percent deviation explained by a given variable; df values for variables
 831 subject to smoothing are approximations only (edf); test statistics are either chi-square (for S_{obs} with
 832 Poisson distribution) or F (for S_{exp} with Gaussian distribution); Curve shape indicates whether a response
 833 was increase (Positive) or decrease (Negative), and whether the shape was a straight line (Linear) or not
 834 (Concave/Increase+plateau).

835

Variable	Dev%	edf	Statistic	p	Curve shape
S_{obs} (n = 91; $R^2 = 0.71$; total deviance = 70.6%)					
Year	0.0	0.0	0.0	0.621	
Country	53.8	6.0	113.6	<0.001	
Forest cover	0.0	1.0	0.1	0.729	
Number of forest patches	1.9	1.0	5.2	0.022	Positive linear
Landscape diversity	3.1	1.0	6.3	0.012	Positive linear
NDVI	1.6	1.8	2.3	0.304	
S_{exp20} (n = 91; $R^2 = 0.47$; total deviance = 53.2%)					
Year	0.0	0.0	0.0	0.480	
Country	32.9	5.2	6.6	<0.001	
Forest cover	2.4	1.0	3.0	0.089	(Negative linear)
Number of forest patches	1.3	1.0	3.2	0.078	(Positive linear)
Landscape diversity	2.6	1.0	4.2	0.045	Positive linear
NDVI	7.7	2.6	3.1	0.020	Concave/Increase+plateau
S_{exp50} (n = 84; $R^2 = 0.55$; total deviance = 60.5%)					
Year	0.0	0.0	0.0	0.668	
Country	36.0	5.4	8.0	<0.001	
Forest cover	1.9	1.0	3.0	0.087	(Negative linear)
Number of forest patches	2.0	1.0	4.5	0.037	Positive linear
Landscape diversity	3.5	1.0	6.2	0.015	Positive linear
NDVI	5.3	2.4	2.0	0.082	(Concave/Increase+plateau)

836

837

838 **Table 2.** GAM results for the species richness of eight ecological groups of birds (for grouping, see
 839 Appendix). For explanatory variables, see Material and methods; Dev% = percent deviation explained by
 840 a given variable; degrees of freedom are approximations only (edf); test statistics are chi-square; Curve
 841 shape indicates whether a response was increase (Positive) or decrease (Negative), and whether the
 842 shape was a straight line (Linear) or not (e.g., Increase+plateau or Convex).

843

Variable	Dev%	edf	Statistic	p	Curve shape
Resident forest species (n = 91; R² = 0.86; total deviance = 85.1%)					
Year	1.3	0.6	2.4	0.051	
Country	51.3	6.6	100.6	<0.001	
Forest cover	7.5	1.0	23.3	0.001	Positive non-linear
Number of forest patches	2.6	1.0	8.1	0.005	Positive linear
Forest diversity	0.3	1.0	0.3	0.779	
NDVI	3.3	2.1	4.7	0.091	(Increase+plateau)
Migratory forest species (n = 80; R² = 0.93; total deviance = 86.0%)					
Year	0.0	0.0	0.0	0.974	
Country	21.1	5.5	60.6	<0.001	
Forest cover	1.7	1.0	5.8	0.017	Positive linear
Number of forest patches	0.5	1.0	1.4	0.240	
Forest diversity	0.0	1.0	0.2	0.633	
NDVI	0.3	1.3	0.2	0.762	
Resident open-habitat species (n = 91; R² = 0.79; total deviance = 73.6%)					
Year	0.0	0.0	0.0	0.451	
Country	28.6	5.4	46.8	<0.001	
Forest cover	6.1	1.0	17.3	<0.001	Negative linear
Number of forest patches	0.4	1.3	0.5	0.764	
Open-habitat diversity	2.6	1.8	6.2	0.060	(Convex)
NDVI	1.4	1.0	3.8	0.052	(Negative linear)
Migratory open-habitat species (n = 91; R² = 0.45; total deviance = 54.5%)					
Year	0.0	0.0	0.0	0.549	
Country	10.1	4.3	14.8	0.001	
Forest cover	21.0	1.7	40.5	<0.001	Negative near-linear
Number of forest patches	0.6	1.5	1.0	0.421	
Open-habitat diversity	1.3	1.0	2.5	0.115	
NDVI	2.4	1.0	6.0	0.014	Negative linear
Resident generalists (n = 79; R² = 0.76; total deviance = 69.4%)					
Year	0.0	0.0	0.0	0.872	
Country	40.4	5.1	32.4	<0.001	
Forest cover	1.0	1.0	1.0	0.310	
Number of forest patches	1.1	1.5	1.2	0.268	
Landscape diversity	0.3	1.0	0.1	0.741	
NDVI	7.6	1.9	6.5	0.043	Increase+plateau
Migratory generalists (n = 74; R² = 0.71; total deviance = 65.7%)					

Year	0.0	0.0	0.0	0.375	
Country	28.8	5.4	30.2	<0.001	
Forest cover	0.6	1.0	1.3	0.245	
Number of forest patches	1.1	1.0	2.2	0.135	
Landscape diversity	0.7	1.0	1.2	0.280	
NDVI	0.4	1.0	0.5	0.502	
Resident urban species (n = 91; R² = 0.77; total deviance = 75.5%)					
Year	0.0	0.0	0.0	0.812	
Country	54.2	6.6	90.0	<0.001	
Forest cover	0.1	1.0	0.1	0.775	
Number of forest patches	1.2	1.0	2.2	0.143	
Landscape diversity	0.8	1.0	0.9	0.333	
NDVI	3.4	1.8	4.1	0.125	
Migratory urban species (n = 68; R² = 0.85; total deviance = 75.0%)					
Year	0.0	0.0	0.0	0.773	
Country	20.1	3.3	20.1	<0.001	
Forest cover	3.0	1.0	2.9	0.109	
Number of forest patches	-0.1	1.0	0.0	0.911	
Landscape diversity	2.1	1.0	3.2	0.075	(Positive linear)
NDVI	4.1	1.8	6.1	0.054	(Concave)

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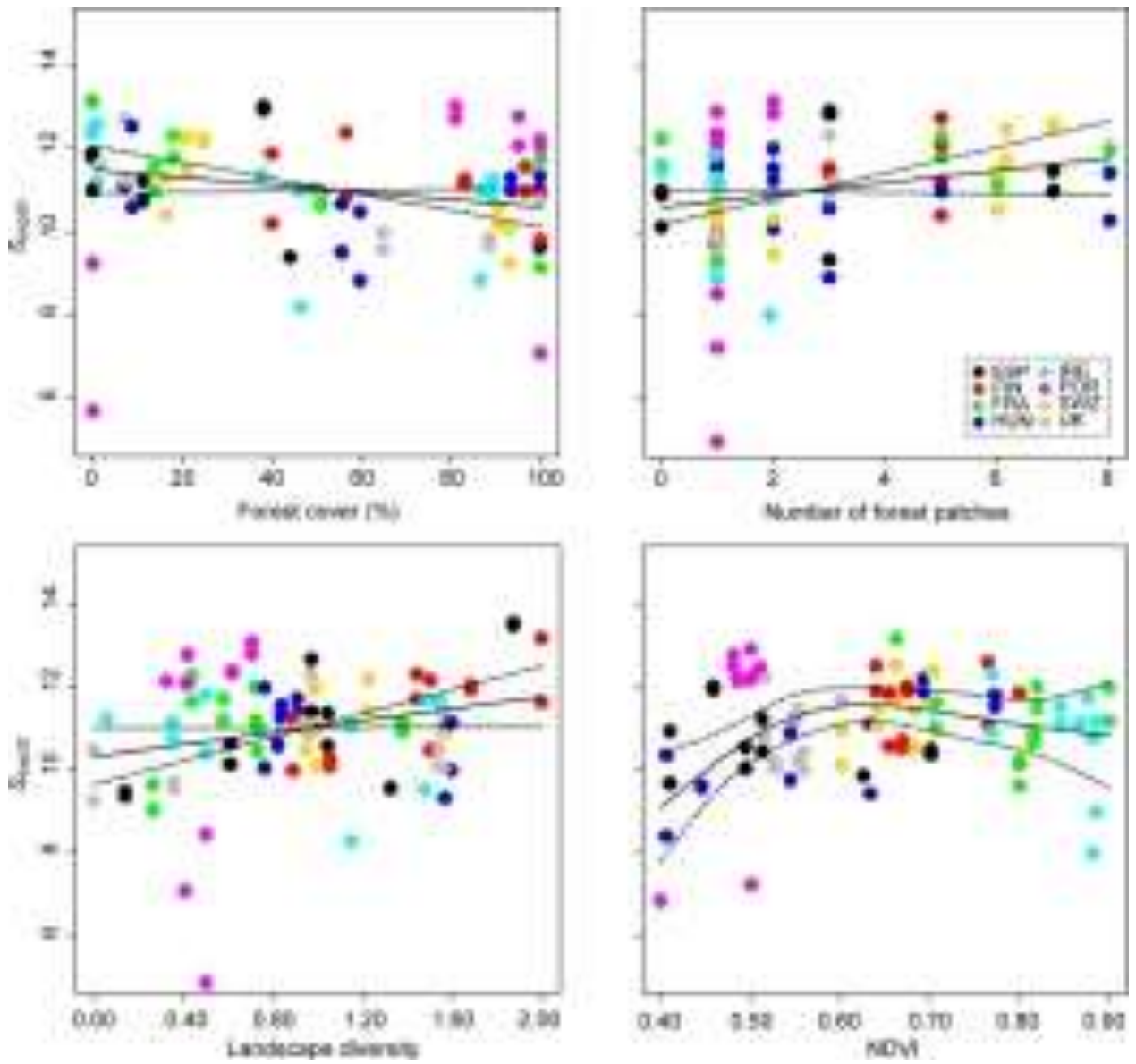
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846 Fig. 1.

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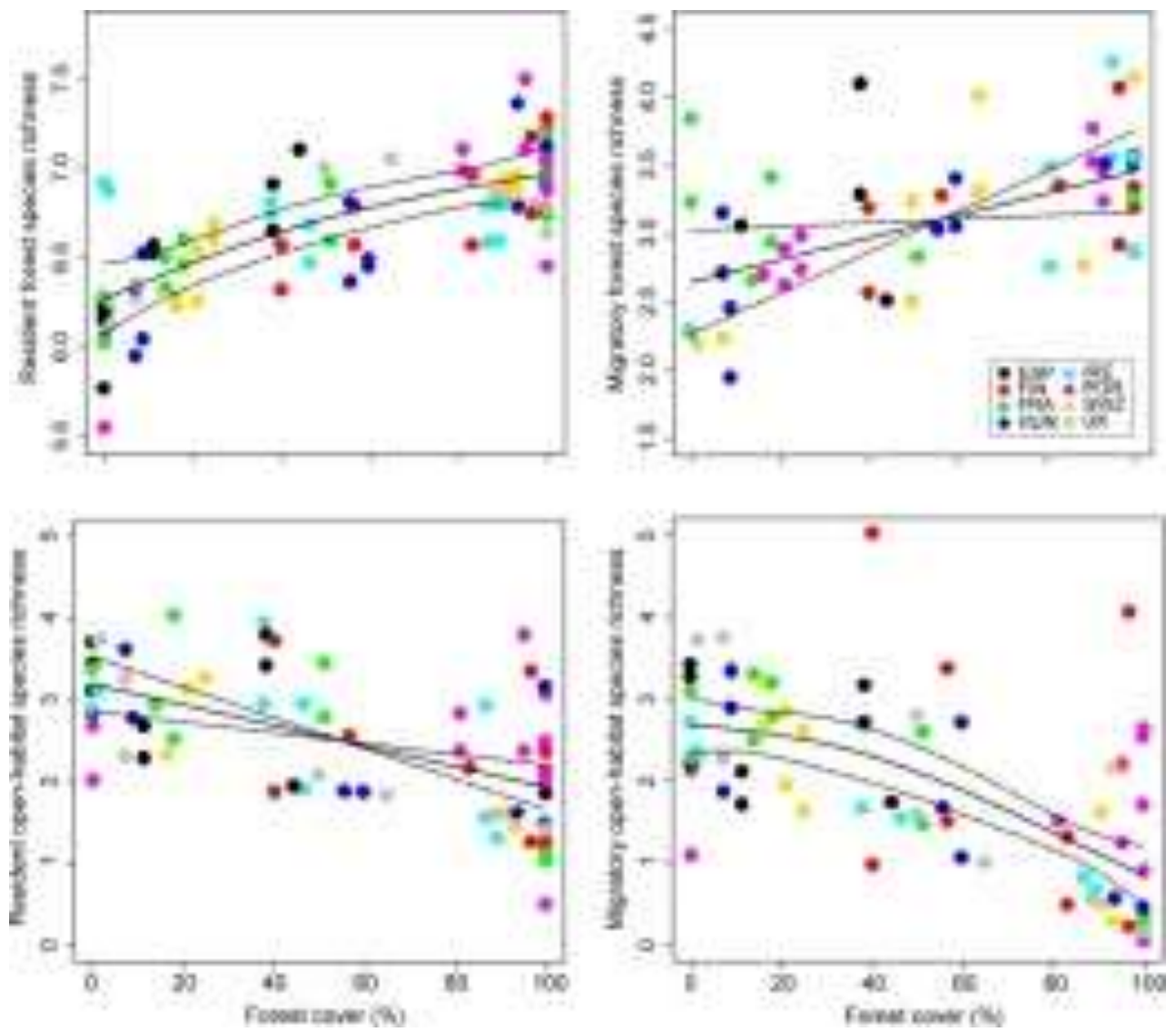
848 Fig. 2.



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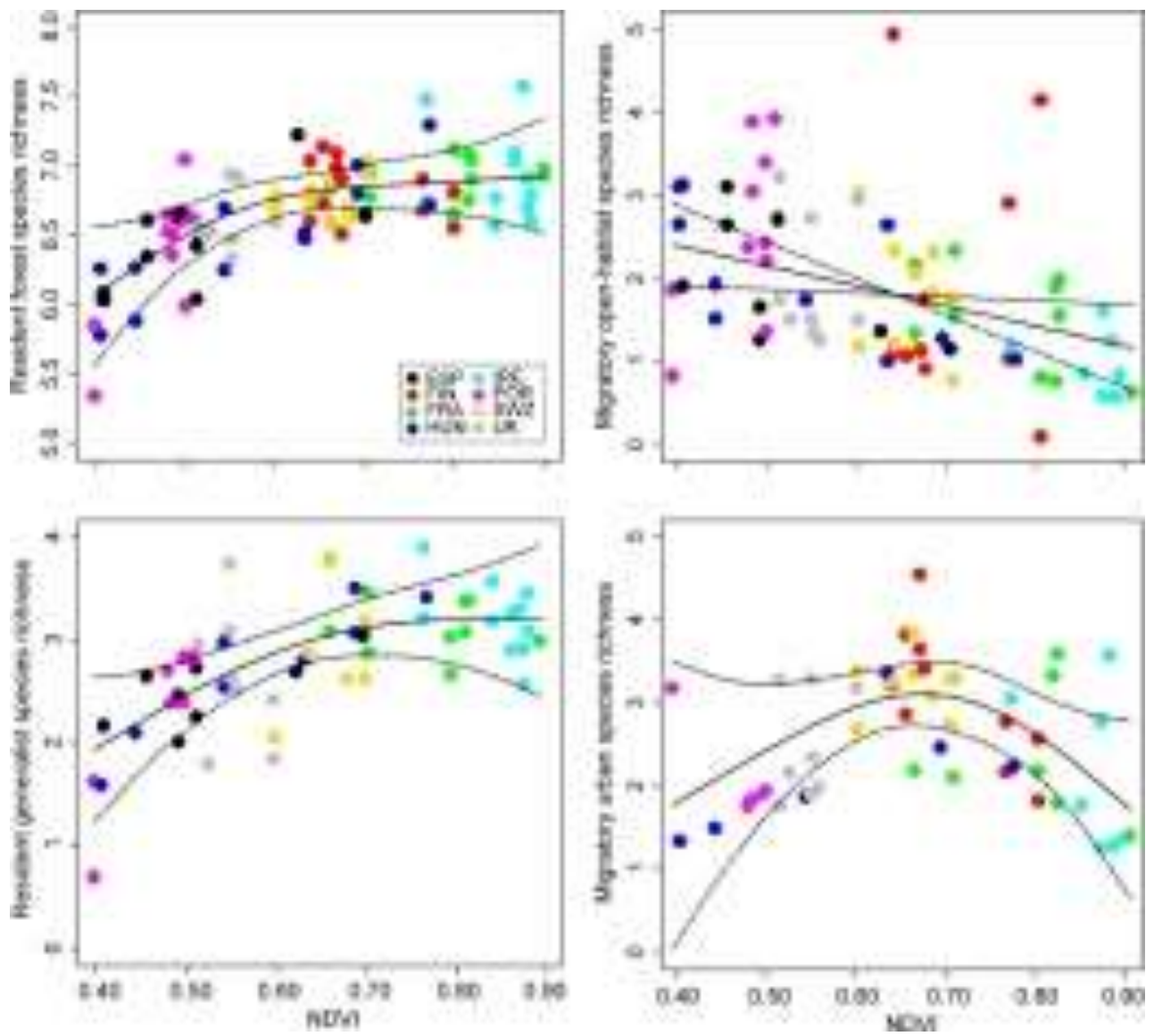
851 Fig. 3.



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854 Fig. 4.



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