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Spatial patterns in habitat specialization of European bird communities

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Highlights

Habitat specialization is predicted to vary along climatic gradients.

We investigated such patterns using breeding bird communities in Europe.

More specialized communities are in areas with more extreme climatic conditions.

Such specialized communities are often, but not always, located at high elevations.

North Scandinavia and steppes north of Caucasus are European specialization hotspots.

Abstract

The level of habitat specialization is informative in terms of animals' population status and conservation concern. Therefore, identifying the areas where specialist species are aggregated and understanding the ecological constraints that might shape their distribution has become an important issue. In this sense, we tested whether specialist communities are more likely to succeed in milder and stable environments or in more extreme and less predictable environments. For that purpose, we used data from the EBCC atlas of European breeding birds and for each of 50 x 50 km grid cells calculated community specialization index (CSI). We expressed CSI in two ways: as a mean (CSI_{MEAN}) and a standard deviation (CSI_{SD}) across species in a given cell. We used generalized least squares (GLS) models to relate these measures to geographic variables (latitude, longitude and altitude) and climatic variables (temperature and rainfall) across Europe controlling for possible confounding effects of habitat heterogeneity and human-induced land cover conversion. We identified two areas, Scandinavian Peninsula and the steppe regions north of Caucasus, where bird communities are highly specialised. GLS models showed that habitat specialization generally increased with altitude and this pattern was broadly shared by the CSI_{MEAN} and CSI_{SD} . Concerning climatic variables, we found that specialist spatial distribution was significantly related to extreme temperatures and lower level of precipitation. Our results thus suggest that European specialist birds are found mostly in strongly seasonal, dry and cold environments. Thereby, preserving these sensible environments from further perturbations might be the key for the specialist conservation.

Keywords

Birds, climate, ecological niche, Europe, habitat specialization, spatial gradient.

1 Introduction

2 Geographical distribution of birds is strongly affected by their habitat selection (Gaston and
3 Blackburn, 2000). Individual species then differ in the level of habitat specialization; i.e. how
4 many biotopes they are able to thrive in. Some species are confined to a single biotope –
5 specialist species, while others are less selective and occupy a wider range of them – generalist
6 species (Futuyma and Moreno, 1988). Avian species show enormous diversity in this respect,
7 which is reflected in the variation of their abundances and extent of geographic ranges (Orme
8 et al., 2006). Habitat specialization thus can be considered as a crucial factor affecting avian
9 diversity patterns in space and not surprisingly attracted a lot of scientific attention (Fuller,
10 2012). Diversity patterns arise as a combination of individual species into communities, which
11 differ in number of co-occurring species (Lennon et al., 2003). As those species are also
12 differently specialised for biotopes (Reif et al., 2016), local avian communities differ in habitat
13 specialization structure, some being on average more specialized than others (Julliard et al.,
14 2006).

15 From a conservation perspective, habitat specialization is a key predictor of population decline
16 (Julliard et al., 2003; Shultz et al., 2005; Le Viol et al., 2012; Sullivan et al., 2016). Therefore, it
17 is not surprising that specialist species has been widely used as bioindicators (Dondina et al.,
18 2017; Ehlers Smith et al., 2018). Identification of the areas of a high community-level
19 specialization can thus provide important information for conservation planning because such
20 areas most likely host numerous species being at risk of extinction. Since habitat specialization
21 is easier to assess than the long-term changes in species' population sizes, an analysis of the
22 community-level habitat specialization at a large spatial scale can be an efficient tool for
23 conservation planning.

24 It is not clear which factors are responsible for overall habitat specialization at the community
25 level. However, intuitively the community specialization should be driven by environmental
26 factors (Pearce-Higgins et al., 2015). Based on the published information, habitat specialization
27 can be linked to environmental stability. For instance, previous studies pointed out how climax
28 stages during the ecological succession tend to support high number of specialists (Devictor *et*
29 *al.*, 2008). On the other hand, other studies suggest that habitat specialization arises from a co-
30 evolutionary process, during which specialists extremely adapt to an environment even if this
31 includes cyclical perturbations that reset the ecological succession (Attum et al., 2006; Clavero
32 et al., 2011; Clavero and Brotons, 2010). However, in the context of global change where
33 extreme environmental events (e.g. droughts, heat waves, floods) are becoming more
34 frequent and less predictable (Jentsch and Beierkuhnlein, 2008), the ecological expenses of
35 being specialised might exceed the benefits (but see Attum et al., 2006).

36 Investigations on large spatial scales offer the previously unexplored opportunity to
37 understand the drivers of community level specialization. We can ask whether the distribution
38 of habitat specialists and generalists show some detectable spatial pattern predicted by
39 environmental parameters. Moreover, recognizing the areas of high concentration of
40 specialized species would aid to uncover sites deserving more attention of conservationists (*cf.*
41 Araújo *et al.*, 2011). Such sites were already identified at a national level (e.g. Devictor *et al.*,
42 2008; Triviño *et al.*, 2013) and estimates of quality of protected areas at European level have
43 been done too (Zupan et al., 2014). However, we are not aware of any attempts to estimate a
44 community level specialisation at the scale of the whole Europe. It is, however, a key
45 perspective because, as a consequence of deep human-induced environmental changes, shifts
46 in species composition took place in ecological communities recently and resulted in an
47 increased dominance of generalists at the expense of specialist species across the European
48 continent (Le Viol *et al.*, 2012). Understanding the continent-level patterns thus might help to

49 prevent local suppression of specialized species or mitigate consequences of the observed
50 trend of biotic homogenisation (Davey et al., 2012; Kerbiriou et al., 2009).

51 Here, we took information about distribution of birds breeding in Europe from Blair &
52 Hagemeyer (1997) and adopted the approach to map community specialization as introduced
53 by Julliard et al. (2006) at the scale of European continent. European birds are particularly
54 suitable for this purpose because their distribution is mapped in adequate detail over the most
55 of the continent (Blair & Hagemeyer, 1997) and were already used in analyses evaluating the
56 state of biodiversity (Gregory et al., 2005; Morelli, 2015). Generally, we did the study with the
57 three main aims. First, to map the distribution of ecological specialization of bird communities
58 across Europe to reveal the continent-level 'hotspots' of specialists.

59 Second, to identify the main environmental drivers of these patterns. Namely, previous studies
60 suggest that geographical distribution of European birds is to large extent determined by
61 climatic conditions (Howard et al., 2015; Huntley et al., 2008; Kopsová-Storchová et al., 2017).
62 Thus, we hypothesize that the large-scale patterns in bird community specialization will be
63 linked to the climatic variability, too. Specifically, with respect to environmental stability we
64 expect two alternative scenarios: (i) more specialized communities occur in more extreme
65 environments (represented by high altitudes, high/low rainfall and temperatures, high climatic
66 seasonality) where specific adaptations of specialists are needed to survive, while generalists
67 would not be able to succeed in those areas (Balasubramaniam and Rotenberry, 2016;
68 Bastianelli et al., 2017); alternatively, (ii) more specialized bird communities occur in milder
69 environments (represented by low altitudes, absence of water and thermal stress, low climatic
70 seasonality) where higher resource availability will provide conditions for coexistence of more
71 specialized species (Seoane et al., 2017).

72 Third, we simultaneously focused on two different measures of community-level
73 specialization: the mean specialization across the species present in the community and the
74 variance of specializations across the species in the community. If the communities of
75 generalists and specialists are spatially segregated (Julliard et al. 2006), we predict that (i) the
76 specialized communities will be in the areas with low variance in specialization, so that (ii) the
77 mean and the variance in specialization will show opposite relationship to the environmental
78 predictors. By contrast, if the generalists and specialists mix in communities of a given level of
79 specialization, we predict that (iii) the mean and the variance in specialization will be positively
80 correlated across bird communities and that (iv) they will show similar relationships to the
81 environmental predictors.

82

83 **2 Material and methods**

84

85 **2.1 Birds' habitat specialization**

86 We extracted information about habitat specialization of each bird species from Reif *et al.*
87 (2016). These authors expressed habitat specialization using species specialization index (SSI).
88 SSI was introduced by Julliard et al. (2006) as a coefficient of variation of species' density
89 across defined set of habitats. Reif et al. (2016) calculated SSI for particular European birds
90 based on the information about their habitat use in Birds of Western Palearctic Interactive
91 (an electronic version of handbooks of Cramp 1977-1994, the most comprehensive species-
92 level information source on ecology of European birds) recognizing species presence or
93 absence in 15 habitats: deciduous forest, coniferous forest, woodland, shrub savannah tundra,
94 grassland, mountain meadow, reed, swamps, semi-desert, freshwater, marine, rocks and

95 human settlements (Storchová and Hořák, 2018). Each species has thus a single “pan-
96 European” SSI value. Reif et al. (2016) did not calculate SSI for species associated to wetlands
97 and aquatic ecosystems (n=221) because these habitats require very specific adaptations and
98 thus their habitat specialization is not comparable to specializations of terrestrial species
99 representing majority of European birds. Moreover, exotic (n=18) and extremely rare (i.e.
100 those occupying less than 20 grid cells in the EBCC Atlas of European breeding birds
101 (Hagemeyer & Blair, 1997), n=28) species were excluded. After this exclusion, we used 252
102 avian species for further analysis.

103 Since our study is based on investigations at the community level, we used information about
104 bird community composition over Europe from The EBCC Atlas of European Breeding Birds
105 (Hagemeyer & Blair, 1997). These data are based on extensive mapping of breeding bird
106 occurrence performed in late 1980s and early 1990s using a UTM grid of 50 × 50 km cells
107 covering major part of the continent. This atlas is still the most recent, detailed and complete
108 source of information about continent-wide distribution of bird species breeding in Europe
109 (e.g. Howard et al. 2015). In total, we extracted data about the presence-absence of our 252
110 focal species in 2059 grid cells covering major part of Europe. In these cells, the quality of data
111 was indicated as high by authors of the Atlas in terms of completeness of species lists
112 (Hagemeyer & Blair, 1997).

113 Based on this presence-absence matrix, we calculated two kinds of community specialization
114 indices (CSI) for each of 50 × 50 km grid cells according to the SSI values of the species present
115 in each cell. First, we calculated a mean of SSIs (hereafter called CSI_{MEAN}) following Julliard et al.
116 (2006). Values of CSI_{MEAN} inform about relative proportion of specialist/generalist species in the
117 bird community occupying each cell. Second, we calculated the standard deviation across SSI
118 values obtaining so called CSI_{SD} . CSI_{SD} informs about variation in specialization across species in
119 the focal bird community. In order to test if our CSI descriptors are species richness
120 dependent, we randomized the community assemblage of each cell by reshuffling the species
121 identities (and therefore the SSIs) but keeping the observed species richness (expressed as the
122 number of bird species recorded as breeding) of each cell. By that means, we obtained
123 randomized CSI values entirely driven by species richness variation. The randomizations were
124 carried out 100 times. Based on these runs, we calculated standardized effect size (SES) of
125 each CSI measure (i.e. CSI_{MEAN} and CSI_{SD}) for each grid cell using formula: $(CSI_{observed} -$
126 $mean(CSI_{simulated}))/standard\ deviation(CSI_{simulated})$. The $SESCSI_{MEAN}$ and $SESCSI_{SD}$ thus show the
127 community specialization corrected for the effect of species richness.

128

129 **2.2 Explanatory variables**

130 For each 50 × 50 km cell containing bird distribution data, we obtained two sets of explanatory
131 variables: geographic and climatic. Geographic variables were the mean altitude of each 50 ×
132 50 km cell, and the longitude and the latitude of the cell’s centre. Climatic variables were
133 temperature and precipitation excerpted from WorldClim database
134 (<http://www.worldclim.org>) as monthly means over the 1961-1990 period. Both temperature
135 and precipitation were expressed as (i) a year-round average across all months (hereafter
136 called ‘temperature mean’ and ‘precipitation mean’) and (ii) a difference between maximum
137 and minimum monthly values, which can be perceived as a measure of seasonality (hereafter
138 called ‘temperature seasonality’ and ‘precipitation seasonality’).

139 Moreover, to control for potential effect of habitat heterogeneity in grid cells and to account
140 for possible influence of anthropogenic habitats, we used data from Corine Land Cover (CLC)
141 database (European Environment Agency, 2007) as areas of particular land cover classes in
142 each 50 × 50 km cell. Since CLC classification contains a high number of land cover classes (44

143 habitat classes) and their classification do not match birds' habitat requirements, we merged
144 the 44 classes into 11 habitat categories well corresponding to the extant information about
145 birds' habitat use (see Cramp 1977-1994): coniferous forest, deciduous forest, mixed forest,
146 woodland, shrubs, grassland, wetlands, freshwater, snow, rocks and anthropogenic habitats
147 (i.e. human settlements, roads, mining areas, industrial areas, cultivated surfaces). For further
148 analysis, we considered only the habitat categories covering at least 1% of the total area of a
149 given cell. Using these data, we calculated (i) Shannon diversity index as a measure of the
150 habitat heterogeneity in each cell and (ii) the coverage of anthropogenic habitats in each cell.
151 These measures were used as additional explanatory variables in statistical analysis.

152

153 **2.3 Statistical analysis**

154 To test the relationships among respective CSI descriptors, we conducted a correlation analysis
155 relating particular CSI descriptors to each other and to the species richness.

156 To identify the geographic patterns in the spatial distribution of the community specialization
157 and their relationships to the climatic conditions, we used generalized least square (GLS)
158 models run in R-package 'nlme' (Pinheiro et al., 2017). The GLS models allow controlling for the
159 spatial autocorrelation, which is inevitably present in spatially explicit data such as ours
160 (Legendre, 1993). We thus introduced various correlation structures of the residuals into the
161 models and assessed their performance by Akaike Information Criterion (AIC). According to the
162 AIC, the best correlation structures were selected.

163 We performed separate sets of analyses with the different CSI descriptors (i.e. CSI_{MEAN} , CSI_{SD}
164 $SECSI_{MEAN}$ and $SECSI_{SD}$) as the respective response variables. Explanatory variables were the
165 geographic and climatic variables described above. Moreover, the habitat heterogeneity and
166 the coverage of anthropogenic habitats were two explanatory variables included in by default
167 all models to control for their possible statistical effects on CSI. Since we expected an
168 association of high community specialization with extreme environments, we used also
169 quadratic terms of mean temperature and precipitation because these terms capture the
170 effects of both negative and positive extremes. Separate sets of GLS models were run for the
171 geographic and for the climatic variables, respectively. Within each set of models, all the
172 possible combinations of variables were assessed according to AIC. As a result, we assessed 7
173 models for the geographical variables and 35 models for the climatic ones (see Table S2 for
174 characteristics of all models run in this study). From these models, we considered only the best
175 performing ones ($\Delta AIC < 2$) for inference. We report the coefficients accompanied by standard
176 errors (SEs) for the variables included in all of these best performing models for each set of
177 analyses. To assess the performance of each variable, we calculated its relative importance
178 (Rel.Imp.) as a sum of Akaike weights of the models where a given variable was included. Note
179 that, since habitat heterogeneity and anthropogenic habitats were coerced into our models to
180 control for their effect, their Rel.Imp. did not have meaningful interpretation and was not
181 calculated for them.

182 To avoid problems with multicollinearity of the explanatory variables, we calculated Pearson
183 correlation coefficient for each pair of geographic and climatic variables, prior the analysis (see
184 Table S1). All coefficients were lower than 0.7 indicating that multicollinearity did not apply to
185 our models. All statistical analyses were conducted in R version 3.3.2 (R Core Team, 2016) and
186 all variables were standardized to zero mean and unit variance before analysis to obtain
187 comparable parameter estimates (Schielzeth, 2010).

188

189 **2.4 Habitat availability**

190 Spatial patterns in CSI may be produced simply by the variation in habitat availability across
191 Europe. In order to test if this effect is present in our data, we conducted a correlation
192 between the middle latitudinal point of the distribution of each species included in the
193 analyses and the number of habitats available in each grid cell (see section 2.2 for description
194 of the habitat data). To be considered as available, the habitat type should cover at least 1% of
195 the total area of the cell. We found a weak positive correlation of habitat availability for each
196 cell with the mid latitudinal point of each species ($r = 0.376$, Fig S1) indicating that slightly
197 more habitats are available for species at higher latitudes.

198

199

200 **3 Results**

201 The SSI ranged from 1.107 ($n = 2$ species; the least specialized ones) to 3.873 ($n = 59$ species;
202 the most specialized ones). Furthermore, most of communities have the same range of the SSI
203 values (2.766). This means that 2023 of the 2059 communities analysed contain at least one
204 specialist species and a generalist one as well.

205 **3.1 Correlations among specialization indices**

206 The correlations among the different CSI descriptors and the species richness (Table 1) showed
207 strong positive correlations between the observed specialization indices (i.e. CSI_{MEAN} and CSI_{SD})
208 and the indices corrected for the effect of species richness (i.e. $SESCSI_{MEAN}$ and $SESCSI_{SD}$)
209 indicating that the species richness did not play a major role in spatial patterns of community
210 specialization across Europe. It was also supported by the absence the relationship between
211 CSI_{MEAN} and species richness and a weakly negative correlation between CSI_{SD} and species
212 richness was (Table 1). Finally, CSI_{MEAN} and CSI_{SD} were positively correlated (Table 1).

213 **3.2 Predictors of CSI_{MEAN} and $SESCSI_{MEAN}$**

214 Within the GLS models containing the geographic variables, both of the best performing
215 models ($\Delta AIC < 2$, Table 2a) for CSI_{MEAN} contained the mean altitude (Rel.Imp = 1.00) and the
216 longitude (Rel.Imp = 0.99). Both of these variables showed positive effects on CSI_{MEAN} (Table
217 3a), i.e. communities were more specialized towards higher altitudes (especially in the
218 Scandinavian Mountains) and longitudes (steppes north of Caucasus), as indicated by Fig. 1a.
219 One model contained also the latitude showing a negative effect on CSI_{MEAN} (Table 3a), but was
220 notably less important (Rel.Imp. = 0.461). In the case of $SESCSI_{MEAN}$, the effects of altitude and
221 longitude were also positive (Table 3a), but generally less important (Rel.Imp. = 0.46 and 0.55,
222 respectively) with altitude present in only one of the best models (Table 2a). Latitude was
223 unimportant (Rel.Imp. = 0.29) and weakly positively related to $SESCSI_{MEAN}$ (Table 3a). These
224 results are in accord with the observation that after correction for species richness, the
225 importance of the Scandinavian “hot spot” of community specialization is less important than
226 the south-eastern European one (Fig. 1a).

227 The most important variables which appeared in all of the best climatic models for CSI_{MEAN}
228 ($\Delta AIC < 2$) were the mean temperature, the mean precipitation and the precipitation
229 seasonality (Rel.Imp. = 1.00, 0.97, 0.79, respectively, Table 2b). The linear term of the mean
230 temperature showed a negative effect, while the effect of precipitation seasonality was
231 positive (Table 3b). The effect of the mean precipitation was dependent of on the presence of
232 its quadratic term being negative when this term was absent (Table 3b). The quadratic term
233 showed a U-shaped relationship between CSI_{MEAN} and precipitation and the same applied to

234 the quadratic term of temperature (Table 3b). Both of these quadratic terms were less
235 important than the linear terms (Rel.Imp = 0.45 and 0.63, respectively). The temperature
236 seasonality was present in two of the best performing models (Rel.Imp = 0.32) showing a weak
237 positive effect on CSI_{MEAN} (Table 3b). After correction of the community specialization for the
238 influence of species richness (i.e. $SESCSI_{MEAN}$), the importance (Rel.Imp = 1.00 and 0.95,
239 respectively) and statistical effects remained unchanged in the case of linear terms of the
240 mean temperature and the mean precipitation (Table 3b). The precipitation seasonality
241 became less important (Rel.Imp. = 0.63), but remained positive (Table 3b). However, the
242 effects of quadratic terms of the mean temperature (Rel.Imp = 0.51) and precipitation (Rel.Imp
243 = 0.33) switched to hump-shaped (Table 3b). Temperature seasonality remained the least
244 important variable (Rel.Imp = 0.28) with a weak positive effect on $SESCSI_{MEAN}$ (Table 3b).

245 **3.3 Predictors of CSI_{SD} and $SESCSI_{SD}$**

246 In the case of CSI_{SD} , only two models showed $\Delta AIC < 2$ for geographic variables (Table 2a). Both
247 contained altitude and latitude (both Rel.Imp = 1.00) with a positive effect on CSI_{SD} (Table 3a).
248 Longitude (Rel.Imp = 0.36) was only in one model showing a positive effect (Table 3a). Analysis
249 of $SESCSI_{SD}$ (Table 2a) confirmed these patterns with high importance of altitude and latitude
250 (both Rel.Imp = 1.00) showing positive effects (Table 3a) and low importance of longitude
251 (Rel.Imp. = 0.01) which was absent in the best model subset (Table 2a). Accordingly, spatial
252 patterns of both CSI_{SD} and $SESCSI_{SD}$ resembled those observed for the mean community
253 specialization, but the high values were more concentrated to Scandinavian Peninsula in
254 norther Europe (Fig. 1c, d).

255 Concerning the climatic models for CSI_{SD} , seven models had $\Delta AIC < 2$ (Table 2b). In all of them,
256 the linear term of the mean temperature was present (Rel.Imp = 1.00, Table 2b) showing a
257 negative effect (Table 3b). Mean precipitation was present in five of the best models (Rel.Imp
258 = 0.65, Table 2b) with a negative effect (Table 3b). The remaining variables were much less
259 important with the quadratic terms of the mean temperature (Rel.Imp. = 0.37) and
260 precipitation (Rel.Imp. = 0.19) showing U-shaped relationships (Table 3b), and the temperature
261 (Rel.Imp. = 0.28) having negative effect and precipitation seasonality (Rel.Imp. = 0.29) positive
262 effect on CSI_{SD} (Table 3b). The analysis of $SESCSI_{SD}$ showed somewhat different patterns with
263 an important hump-shaped effect of temperature (Table 3d) present in all of the best models
264 (Rel.Imp. = 1.00 and 0.90 for linear and quadratic term, respectively; Table 2b). The mean
265 precipitation (Rel.Imp. = 0.41) was present in only one of the best models (Table 2b) with a
266 weak negative effect (Table 3b) and the quadratic term of the mean precipitation (Rel.Imp. =
267 0.11) did not appear in the best models at all (Table 2b). On the other hand, the importance
268 (Rel.Imp. = 0.28 and 0.38, respectively) and the effects of the seasonality in temperature and
269 precipitation were very similar to the results obtained for CSI_{SD} (Table 3b).

270 **3.4 Influence of habitat heterogeneity and anthropogenic habitats**

271 To control for possible effects of habitat heterogeneity and the cover of anthropogenic
272 habitats on community specialization, we included their descriptors in all models. Their
273 coefficients and SEs indicate that they were unrelated to any of the CSI measures (Table 3).

274

275 **4 Discussion**

276

277 Our analysis of the spatial distribution of bird community specialization across Europe
278 uncovered following relationships: (i) CSI_{MEAN} and CSI_{SD} are positively correlated, both showing
279 high values in Scandinavia and in the area north of Caucasus. (ii) Both CSI_{MEAN} and CSI_{SD}
280 increase towards higher altitudes; CSI_{MEAN} also increases along the longitudinal gradient and
281 CSI_{SD} along the latitudinal gradient, whereas latitude plays a minor role for CSI_{MEAN} and
282 longitude for CSI_{SD} . (iii) Cold temperatures and lower levels of precipitation characterize areas
283 with high values of both CSI_{MEAN} and CSI_{SD} . (iv) In addition, high seasonality in rainfall regime
284 and the U-shape function of temperate are related to high CSI_{MEAN} values, but much less so in
285 the case of CSI_{SD} . (v) The patterns in community specialization are largely independent of
286 the species richness since it was unrelated to both specialization indices and the main
287 relationships remained qualitatively unchanged if $SESCSI_{MEAN}$ $SESCSI_{SD}$ were considered instead
288 of CSI_{MEAN} and CSI_{SD} . (vi) However, some changes occurred in the minor patterns: removing the
289 effect of species richness from CSI indices further decreased the importance of the latitude for
290 CSI_{MEAN} , the longitude for CSI_{SD} and the climatic seasonality for both measures putting more
291 weight to the mean values of the climatic gradients. The randomization procedure further
292 suggests that assemblages in central parts of Europe are less specialized than expected by
293 chance, which does not apply to northern latitudes. (vii) We did not find evidence that the
294 human modification and the heterogeneity of habitat play a major role in the spatial patterns
295 in community specialization at the scale of resolution of our study.

296

297 The broad congruence between the spatial patterns in CSI_{MEAN} and CSI_{SD} suggests that, at the
298 spatial scale of our dataset, increasing community specialization is not accompanied with
299 spatial segregation of generalist and specialist communities. This pattern and the fact that
300 generalist species are present in all the studied communities support the idea that CSI_{MEAN}
301 variability relies on the aggregation of specialists. This finding does not correspond with an
302 earlier study from France showing such a spatial segregation of specialists and generalists
303 (Julliard et al., 2006). However, we suggest that these differences between studies can be
304 explained by differences in spatial scales of the datasets: whereas Julliard et al. (2006) worked
305 with local bird monitoring data, we used relatively large squares of 50 x 50 km. Even if habitat
306 specialists and generalists are segregated locally, this fine-scale segregation obviously does not
307 scale up to larger areas. These relatively large spatial units used for sampling of bird
308 communities in our dataset are also likely responsible for the absence of the relationships
309 between the community specialization measures and habitat heterogeneity and proportion of
310 anthropogenic habitats, respectively. It is possible that the diversity of habitats would affect
311 the distribution of specialist species locally (Reif et al., 2013), but the large grid cells used in
312 this study frequently contain a mixture of many habitats, so the patterns in habitat
313 specialization observed in our data result from large-scale climatic gradients as discussed in
314 the paragraphs below. Similarly, large cell size likely mitigated the effects of the human impact
315 as expressed in our dataset: it is possible that even the areas dominated by human influence
316 contained some sites with natural environment where specialized species may occur.

317 Our results suggest that bird communities containing specialized species are generally
318 associated with cold, highly seasonal and extreme environments, i.e. in accord with our first
319 expected scenario, and not with mild and stable environments as predicted the alternative.
320 This finding is somewhat surprising as, according to the resource specialization hypothesis as a
321 part of species-energy theory, mild and stable conditions should lead to the fine division of
322 resources among species, resulting in the evolution of narrow habitat niches and thus densely-
323 packed species-rich communities (Evans *et al.*, 2006; Seoane et al. 2017). In contrast, according
324 to our data, rougher, and not milder environmental conditions force the species to have a
325 certain degree of specialization. From this perspective, specialists are the species occupying
326 environments where other species are not able to exist, i.e. the extremes. This is consistent

327 with the view of specialists' communities as those being under pressure of strong
328 environmental filters and thus being relatively species-poor (Ducatez et al., 2014; Šizling et al.,
329 2009).

330 Yet the question remains, why avian specialist communities show affinity to rougher climates?
331 From an evolutionary perspective, in European bird fauna, broad habitat niche was among the
332 adaptations selected by orbitally forced range dynamics to survive the Quaternary climatic
333 oscillations (Dynesius and Jansson, 2000). From this perspective, high seasonality should
334 favour existence of habitat generalists, i.e. the opposite to the pattern we found. One
335 explanation may be that the extant European species are all "generalists" from this historical
336 perspective since the "real specialists" were lost during the past oscillations in the temperate
337 zone (and are now possibly confined to the tropics, see Blondel, 1997). Therefore, here we
338 probably study different levels of habitat specialization within such "historical generalists".
339 Among these species, and considering an ecological time frame, we suggest that the link
340 between habitat specialization and high climatic seasonality observed in our data is caused by
341 the fact, that the habitats in these climates require some specific adaptations. This makes the
342 species confined to their specific habitat and preclude the occupation of the other habitats.
343 For example, species confined to the boreal or high-altitude forest (e.g. Siberian Jay (*Perisoreus*
344 *infaustus*) or Capercaillie (*Tetrao urogallus*), Mikoláš et al., 2017) do not breed in tundra or
345 alpine grasslands and vice versa (e.g. Snow Bunting (*Plectrophenax nivalis*) or Water Pipit
346 (*Anthus spinoletta*), Melendez & Laiolo, 2014). In contrast, species found in temperate forest
347 are mostly generalists breeding in a variety of woody habitats from forest interior to small
348 woodlots, grassland-shrubland mosaics or even urban environment (e.g. Robin (*Erithacus*
349 *rubecula*), Blackcap (*Sylvia atricapilla*) or Woodpigeon (*Columba palumbus*), Reif et al., 2016).
350 We do not know, what are the supposed adaptations in these cases but we suggest that they
351 may concern food requirements (such as bilberry for Capercaillie, see Storch, 1993).

352 Focusing on the geographic drivers, we are aware that extreme climatic conditions are typical
353 for high altitudes (Körner, 2007) and thus the increase of CSI descriptors with the altitude can
354 be partly attributable to higher extremeness of climate towards higher elevations. However,
355 the effect of altitude may be important even besides the effects of temperature and
356 precipitation. Moreover, the peaks of CSI were mostly confined to montane areas
357 (Scandinavian Mountains, Alps, Carpathians) indicating that montane conditions are very
358 specific and this specificity cannot be fully attributed to climate. We suggest that one factor
359 responsible for the montane exceptionalism may be relatively small area of high elevations
360 within Europe (European Environment Agency, 2002). Such a rarity of montane environment
361 can thus by itself lead to high habitat specialization of birds inhabiting this environment. As
362 another explanation (not mutually exclusive) may serve the pressure of oxygen declining
363 towards higher altitudes resulting in higher metabolic demands (Körner, 2007) and thus
364 leading to evolution of specific life history strategies to survive in high mountains
365 (Balasubramaniam and Rotenberry, 2016; Bastianelli et al., 2017). Such specific strategies
366 involve larger clutch size and longer parental care which are, in turn, not advantageous under
367 milder conditions where other pressures (e.g. higher predation rate due to higher diversity of
368 predators) compromise the advantages (Bastianelli et al., 2017). Given these constrains,
369 species being able to survive in high mountains will also specialize to montane environment in
370 terms of habitat use (Laiolo et al., 2015).

371 It is interesting that the associations of the high CSI values with seasonality in precipitation and
372 extreme temperatures were represented by the "cold" or "north" (northern Scandinavia), as
373 well as by the "hot" or "south" extreme (norther Caucasus regions). Based on the location of
374 the European continent within the northern temperate zone, one would expect that its
375 territory will sample the northern extreme but not the extremely hot and dry seasonal
376 climates - specialists to these environments would breed further south in Africa. Instead,

377 spatial distribution of CSI values clearly shows that this is not the case here. It seems that the
378 climatic conditions in steppe region of south-eastern Europe in the front of Caucasus are
379 sufficiently extreme to select for high habitat specialization. This finding also stresses the
380 importance for including the Eastern parts of Europe, which are often difficult to cover by
381 relevant biological information due to the lack of citizen scientists (Kalyakin & Voltzit, 2013),
382 into macroecological continent-wide studies to avoid bias in data and flawed inference
383 (Sutcliffe et al., 2015).

384 After taking the effect of species richness into account, the importance of the latitudinal
385 gradient, mean temperatures and climatic seasonality declined for CSI_{MEAN} . It accords with the
386 observation of a lower specialization of bird assemblages in Central Europe than would be
387 expected according to the species richness, which was not the case for northern latitudes (Fig.
388 2b). In other words, as bird species richness increases from Northern to Central Europe, the
389 enrichment of bird communities is driven by adding of generalist species. Mechanisms
390 responsible for occurrence of such species in this region are unclear, but we can speculate
391 about some kind of human modification of landscape favouring generalists, which has not
392 been addressed in our analysis. For instance, Central European landscape shows the highest
393 degree of habitat fragmentation from all European countries with adverse consequence for
394 biodiversity (Konvicka et al., 2006) which may favour the presence of generalist species. In the
395 case of CSI_{SD} , a negative effect of species richness could be expected since the standard
396 deviation inevitably increases with reduction of the sample size. Although we found a weak
397 negative correlation between these two measures in our dataset, the latitudinal gradient in
398 CSI_{SD} was indeed stronger after removing the influence of species richness. Taken together, our
399 results indicate that the main spatial patterns in community specialization across Europe are
400 largely independent of species richness, but it obviously influenced some variation in
401 community specialization at the same time.

402 We showed for the first time, a large-scale gradients of habitat specialization for bird
403 communities across the European continent. Our results indicate that several “hot spots” for
404 European birds’ community specialization are located in northernmost part of the continent
405 and in the steppe region of south-eastern Europe, probably because climatic extremeness
406 selects for specific adaptations to local conditions. However, we also detected several other
407 regions with particularly high values of CSI (montane regions such as Alps and Carpathians).
408 Such areas deserve attention of conservationists because habitat specialization is a strong
409 predictor of species’ population decline and extinction risk (Clavel et al., 2011; Koleček et al.,
410 2014; Owens and Bennett, 2000) Although the network of protected areas is relatively well-
411 developed in Europe, it does not apply to many regions especially in Eastern Europe (Sutcliffe
412 et al., 2015) where we recommend focusing the conservation effort on the areas of the CSI we
413 identified here. Moreover, the establishment a protected area does not guarantee the
414 effective conservation if the level of enforcement is low, which is the case even in some EU-
415 countries (Ioja et al., 2010). For example, the loss of old-growth forest habitat is widespread
416 across Carpathians irrespective of the existence of protected areas (Sabatini et al., 2018). Our
417 results highlight the uniqueness of the montane areas in terms of habitat specialization and
418 thus quest for better protection in regions where it seems not yet sufficient.

419 However, we are aware of our study limitations when it comes to conservation implications,
420 namely its relatively coarse spatial resolution with the basic spatial units of 50 x 50 km used for
421 the analysis. At this resolution, we cannot sample local habitat composition to infer its impact
422 on the bird community assembly, which can be highly relevant for planning of the local
423 conservation actions. Instead, our study provides guidance for determination of the regions
424 where communities with high proportion of specialist exist, and what are their climatic and
425 geographic determinants. Our results can be thus used for setting the continent-level
426 conservation priorities, but not for specification of the local management plans. The next

427 caveat of our study is the insufficient coverage of some European regions by the data on bird
428 distribution (see maps in Hagemejjer and Blair, 1997). Specifically, our “hot spot” of
429 specialization located north of Caucasus is surrounded by extensive areas, especially in eastern
430 direction, where data on bird breeding occurrence are lacking. It is thus possible that some
431 more “hot spots” are indeed hidden in these unsampled areas. It is promising that the co-
432 ordinators of the new European bird distribution atlases, planned to be published in the
433 forthcoming decade, make effort to cover the localities where the data are currently missing
434 (Herrando et al., 2017). Their analysis may be a subject of the future studies.

435 Summarizing, our results support the hypothesis that specialized communities of birds inhabit
436 climatically extreme conditions in Europe, presumably because of specific habitat types, where
437 special ecological adaptations are required. The remaining question is whether such specialists
438 cannot live under milder climates because of their low competitive ability or whether they take
439 advantage of the situation when freed ecological space under such extreme conditions is
440 affordable for certain species only. The first case would be especially alarming as climatic
441 change might strongly affect range spreading potential of populations in such specialized
442 species (Koschová et al., 2014).

443

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448

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639 **Table 1.** Correlations among specialization indices of bird communities (CSI) consisting of species recorded as breeding in 50 x 50 km mapping squares and
 640 the species richness across Europe. CSI_{MEAN} – mean of habitat specialization across the species in a given bird community; $SESCSI_{MEAN}$ – standardized effect
 641 size of CSI_{MEAN} revealed by controlling for the effect of the species richness; CSI_{SD} – standard deviation of the habitat specialization across the species in a
 642 given bird community; $SESCSI_{SD}$ – standardized effect size of CSI_{MEAN} revealed by controlling for the effect of the species richness; species richness – number
 643 of species recorded in a given bird community. See Methods section for more details on definitions of particular variables.

	CSI_{SD}	Species richness	$SESCSI_{MEAN}$	$SESCSI_{SD}$
CSI_{MEAN}	0.72	0.06	0.87	0.63
CSI_{SD}	1.00	-0.26	0.77	0.95

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648 **Table 2.** Characteristics of the best performing generalised least squares models ($\Delta AIC < 2$) relating the specialization indices of bird communities (CSI)
649 consisting of species recorded as breeding in 50 x 50 km mapping squares to (a) geographic variables and (b) climatic variables over Europe. CSI_{MEAN} – mean
650 of habitat specialization across the species in a given bird community; $SESCSI_{MEAN}$ – standardized effect size of CSI_{MEAN} revealed by controlling for the effect
651 of the species richness; CSI_{SD} – standard deviation of the habitat specialization across the species in a given bird community; $SESCSI_{SD}$ – standardized effect
652 size of CSI_{MEAN} revealed by controlling for the effect of the species richness. See Methods section for more details on definitions of particular variables.

653

a) geographic variables

Model name	Model terms	df ⁽¹⁾	R ²⁽²⁾	ΔAIC ⁽³⁾	AIC weight
CSI_{MEAN}					
Mean_gm1	$CSI_{MEAN} \sim \text{altitude}^{(4)} + \text{longitude}^{(5)} + \text{Heterogeneity}^{(6)} + \text{Anthropogenic}^{(7)}$	8	0.50	0.00	0.54
Mean_gm2	$CSI_{MEAN} \sim \text{altitude} + \text{latitude}^{(8)} + \text{longitude} + \text{Heterogeneity} + \text{Anthropogenic}$	9	0.34	-0.31	0.46
$SESCSI_{MEAN}$					
SESM_gm1	$SESCSI_{MEAN} \sim \text{longitude} + \text{Heterogeneity} + \text{Anthropogenic}$	7	0.45	0.000	0.382
SESM_gm2	$SESCSI_{MEAN} \sim \text{altitude} + \text{Heterogeneity} + \text{Anthropogenic}$	7	-0.05	-0.39	0.315
SESM_gm3	$SESCSI_{MEAN} \sim \text{latitude}^{(8)} + \text{longitude} + \text{Heterogeneity} + \text{Anthropogenic}$	8	0.48	-1.89	0.149
CSI_{SD}					
SD_gm1	$CSI_{SD} \sim \text{altitude} + \text{latitude} + \text{Heterogeneity} + \text{Anthropogenic}$	8	0.16	0.00	0.64
SD_gm2	$CSI_{SD} \sim \text{altitude} + \text{latitude} + \text{longitude} + \text{Heterogeneity} + \text{Anthropogenic}$	9	0.25	-1.16	0.36
$SESCSI_{SD}$					
SESS_gm1	$SESCSI_{SD} \sim \text{altitude} + \text{latitude} + \text{Heterogeneity} + \text{Anthropogenic}$	8	0.58	0.00	0.99

b) climatic variables

Model name	Model	df ⁽¹⁾	R ²⁽²⁾	ΔAIC ⁽³⁾	AIC weight
CSI_{MEAN}					
Mean_cm1	CSI _{MEAN} ~ temp_mean ⁽⁹⁾ + temp^2 ⁽¹⁰⁾ + prec_mean ⁽¹¹⁾ + prec_seas ⁽¹²⁾ + Heterogeneity + Anthropogenic	10	0.43	0.00	0.20
Mean_cm2	CSI _{MEAN} ~ temp_mean + temp^2 + prec_mean + prec2 ⁽¹³⁾ + prec_seas + Heterogeneity + Anthropogenic	11	0.42	0.81	0.13
Mean_cm3	CSI _{MEAN} ~ temp_mean + temp^2 + prec_mean + temp_seas ⁽¹⁴⁾ + prec_seas + Heterogeneity + Anthropogenic	11	0.46	1.27	0.11
Mean_cm4	CSI _{MEAN} ~ temp_mean + prec_mean + prec_seas + Heterogeneity + Anthropogenic	9	0.45	1.42	0.10
Mean_cm5	CSI _{MEAN} ~ temp_mean + prec_mean + prec^2 + prec_seas + Heterogeneity + Anthropogenic	10	0.44	1.50	0.09
Mean_cm6	CSI _{MEAN} ~ temp_mean + temp^2 + prec_mean + prec^2 + temp_seas + prec_seas + Heterogeneity + Anthropogenic	12	0.46	1.81	0.08
SESCSI_{MEAN}					
SESM_cm1	SESCSI _{MEAN} ~ temp_mean + temp2 + prec_mean + prec_seas + Heterogeneity + Anthropogenic	10	0.47	0.00	0.14
SESM_cm2	SESCSI _{MEAN} ~ temp_mean + prec_mean + prec_seas + Heterogeneity + Anthropogenic	9	0.45	0.17	0.13
SESM_cm3	SESCSI _{MEAN} ~ temp_mean + temp2 + prec_mean + Heterogeneity + Anthropogenic	9	0.50	0.17	0.13
SESM_cm4	SESCSI _{MEAN} ~ temp_mean + prec_mean + prec2 + prec_seas + Heterogeneity + Anthropogenic	10	0.46	0.97	0.09
SESM_cm5	SESCSI _{MEAN} ~ temp_mean + temp2 + prec_mean + prec2 + prec_seas + Heterogeneity + Anthropogenic	11	0.48	1.24	0.08
Mean_cm6	SESCSI _{MEAN} ~ temp_mean + prec_mean + Heterogeneity + Anthropogenic	8	0.47	1.31	0.07
Mean_cm7	SESCSI _{MEAN} ~ temp_mean + temp2 + prec_mean + temp_seas + prec_seas + Heterogeneity + Anthropogenic	11	0.49	1.77	0.06
Mean_cm8	SESCSI _{MEAN} ~ temp_mean + prec_mean + prec2 + Heterogeneity + Anthropogenic	9	0.48	1.92	0.05
Mean_cm9	SESCSI _{MEAN} ~ temp_mean + prec_mean + temp_seas + prec_seas + Heterogeneity + Anthropogenic	10	0.47	1.97	0.05

CSI_{SD}					
SD_cm1	CSI _{SD} ~ temp_mean + prec_mean + Heterogeneity + Anthropogenic	8	0.62	0.00	0.15
SD_cm2	CSI _{SD} ~ temp_mean + Heterogeneity + Anthropogenic	7	0.63	0.66	0.11
SD_cm3	CSI _{SD} ~ temp_mean + temp^2 + prec_mean + Heterogeneity + Anthropogenic	9	0.64	1.07	0.09
SD_cm4	CSI _{SD} ~ temp_mean + temp^2 + Heterogeneity + Anthropogenic	8	0.64	1.53	0.07
SD_cm5	CSI _{SD} ~ temp_mean + prec_mean + prec_seas + Heterogeneity + Anthropogenic	9	0.62	1.67	0.07
SD_cm6	CSI _{SD} ~ temp_mean + prec_mean + prec^2 + Heterogeneity + Anthropogenic	9	0.62	1.87	0.06
SD_cm7	CSI _{SD} ~ temp_mean + prec_mean + temp_seas + Heterogeneity + Anthropogenic	9	0.62	1.92	0.06
SESCSI_{SD}					
SESS_cm1	SESCSI _{SD} ~ temp_mean + temp2 + Heterogeneity + Anthropogenic	8	0.62	0.00	0.25
SESS_cm2	SESCSI _{SD} ~ temp_mean + temp2 + prec_seas + Heterogeneity + Anthropogenic	9	0.61	1.17	0.14
SESS_cm3	SESCSI _{SD} ~ temp_mean + temp2 + prec_mean + Heterogeneity + Anthropogenic	9	0.61	1.52	0.12
SESS_cm4	SESCSI _{SD} ~ temp_mean + temp2 + temp_seas + Heterogeneity + Anthropogenic	9	0.62	1.94	0.10

654 ⁽¹⁾ Degrees of freedom

655 ⁽²⁾ Coefficient of determination expressed as the squared Pearson correlation coefficient between the predicted and observed values.

656 ⁽³⁾ Difference in values of the Akaike Information Criterion (AIC) between a given model and the best performing model.

657 ⁽⁴⁾ mean altitude in a given mapping square

658 ⁽⁵⁾ longitude of the centre of a given mapping square

659 ⁽⁶⁾ Shannon diversity index for the number of habitats available in a given mapping square

660 ⁽⁷⁾ Coverage of habitats with anthropogenic origin in a given mapping square

- 661 ⁽⁸⁾ Latitude of the centre of a given mapping square
- 662 ⁽⁹⁾ Linear term of mean temperature in a given mapping square
- 663 ⁽¹⁰⁾ Quadratic term of mean temperature in a given mapping square
- 664 ⁽¹¹⁾ Linear term of mean precipitation in a given mapping square
- 665 ⁽¹²⁾ Precipitation seasonality in a given mapping square
- 666 ⁽¹³⁾ Quadratic term of mean precipitation in a given mapping square
- 667 ⁽¹⁴⁾ Temperature seasonality in a given mapping square
- 668

669 **Table 3.** The coefficients (Coef) and standard errors (SE) of particular predictor variables revealed by best performing generalised least squares models (ΔAIC
670 < 2) relating the specialization indices of bird communities (CSI) consisting of species recorded as breeding in 50 x 50 km mapping squares to (a) geographic
671 variables and (b) climatic variables over Europe. CSI_{MEAN} – mean of habitat specialization across the species in a given bird community; $SESCSI_{MEAN}$ –
672 standardized effect size of CSI_{MEAN} revealed by controlling for the effect of the species richness; CSI_{SD} – standard deviation of the habitat specialization across
673 the species in a given bird community; $SESCSI_{SD}$ – standardized effect size of CSI_{MEAN} revealed by controlling for the effect of the species richness. See
674 Methods section for more details on definitions of particular variables.

675

a) Geographic variables										
	Altitude ⁽¹⁾		Latitude ⁽²⁾		Longitude ⁽³⁾		Heterogeneity ⁽⁴⁾		Anthropogenic ⁽⁵⁾	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE
CSI_{MEAN}										
Mean_gm1	0.00002	0.000004	-	-	0.002	0.001	0.004	0.008	-0.00001	0.00004
Mean_gm2	0.00002	0.000004	-0.001	0.001	0.002	0.001	0.006	0.008	-0.00001	0.00005
$SESCSI_{MEAN}$										
SESM_gm1	-	-	-	-	0.022	0.008	-0.020	0.105	-0.0001	0.001
SESM_gm2	0.0001	0.0001	-	-	-	-	-0.017	0.105	0.0003	0.001
SESM_gm3	-	-	0.004	0.012	0.021	0.008	-0.025	0.106	-0.0001	0.001
CSI_{SD}										
SD_gm1	0.00002	0.000003	0.002	0.001	-	-	0.004	0.005	-0.00004	0.00003
SD_gm2	0.00002	0.000003	0.002	0.001	0.0005	0.0004	0.005	0.005	-0.00004	0.00003
$SESCSI_{SD}$										

SESS_gm1	0.0004	0.0001	0.056	0.015	-	-	0.057	0.152	-0.001	0.001
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b) Climatic Variables

	Temperature Mean ⁽⁶⁾		Temperature ² ⁽⁷⁾		Temperature Seasonality ⁽⁸⁾		Precipitation Mean ⁽⁹⁾		Precipitation ² ⁽¹⁰⁾		Precipitation Seasonality ⁽¹¹⁾		Heterogeneity		Anthropogenic	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE
CSI_{MEAN}																
Mean_cm1	-0.008	0.008	-0.012	0.006	-	-	-0.007	0.003	-	-	0.007	0.003	0.001	0.002	-0.001	0.001
Mean_cm2	-0.009	0.008	-0.011	0.006	-	-	0.001	0.008	-0.007	0.007	0.007	0.003	0.001	0.002	-0.001	0.001
Mean_cm3	-0.008	0.008	-0.012	0.006	0.005	0.005	-0.006	0.003	-	-	0.007	0.003	0.001	0.002	-0.001	0.001
Mean_cm4	-0.021	0.003	-	-	-	-	-0.007	0.003	-	-	0.006	0.003	0.001	0.002	-0.001	0.001
Mean_cm5	-0.02	0.004	-	-	-	-	0.003	0.008	-0.009	0.007	0.007	0.003	0.001	0.002	-0.001	0.001
Mean_cm6	-0.009	0.008	-0.01	0.006	0.005	0.006	0.003	0.008	-0.008	0.007	0.008	0.003	0.001	0.002	-0.001	0.001
SESCSI_{MEAN}																
SESM_cm1	-0.068	0.022	0.002	0.001	-	-	-0.0003	0.0001	-	-	0.005	0.003	-0.021	0.104	0.0000	0.001
SESM_cm2	-0.039	0.010	-	-	-	-	-0.0003	0.0001	-	-	0.006	0.003	-0.011	0.104	0.0000	0.001
SESM_cm3	-0.069	0.022	0.002	0.001	-	-	-0.0003	0.0001	-	-			-0.019	0.104	-0.0001	0.001
SESM_cm4	-0.041	0.010	-	-	-	-	-0.001	0.0004	0.0000002	0.0000002	0.006	0.003	-0.020	0.104	-0.0001	0.001
SESM_cm5	-0.067	0.022	0.002	0.001	-	-	-0.001	0.0004	0.0000001	0.0000002	0.005	0.003	-0.028	0.105	-0.0001	0.001
SESM_cm6	-0.034	0.010	-	-	-	-	-0.0003	0.0001	-	-			-0.006	0.104	-0.0001	0.001
SESM_cm7	-0.068	0.022	0.002	0.001	0.02	0.041	-0.0003	0.0001	-	-	0.005	0.003	-0.018	0.104	-0.0001	0.001

SESM_cm8	-0.036	0.010	-	-	-	-	-0.001	0.0004	0.0000002	0.0000002			-0.017	0.104	-0.0002	0.001
SESM_cm9	-0.039	0.010	-	-	0.018	0.041	-0.0003	0.0001	-	-	0.006	0.003	-0.008	0.104	0.0000	0.001
CSI_{SD}																
SD_cm1	-0.004	0.0005	-	-	-	-	-0.00001	0.00001	-	-	-	-	0.005	0.005	-	0.00003
SD_cm2	-0.004	0.0005	-	-	-	-	-	-	-	-	-	-	0.005	0.005	-	0.00003
SD_cm3	-0.005	0.001	0.00006	0.00006	-	-	-0.00001	0.00001	-	-	-	-	0.005	0.005	-	0.00003
SD_cm4	-0.005	0.001	0.0001	0.0001	-	-	-	-	-	-	-	-	0.005	0.005	-	0.00003
SD_cm5	-0.004	0.001	-	-	-	-	-0.00001	0.00001	-	-	0.0001	0.0002	0.005	0.005	-	0.00003
SD_cm6	-0.004	0.0005	-	-	-	-	-	0.00002	0.00000001	0.00000001	-	-	0.005	0.005	-	0.00003
SD_cm7	-0.004	0.0005	-	-	-0.001	0.002	-0.00001	0.00001	-	-	-	-	0.005	0.005	-	0.00003
SESCSI_{SD}																
SESS_cm1	-0.155	0.030	0.005	0.002	-	-	-	-	-	-			0.071	0.150	-0.001	0.001
SESS_cm2	-0.153	0.030	0.004	0.002	-	-	-	-	-	-	0.004	0.005	0.067	0.151	-0.001	0.001
SESS_cm3	-0.156	0.030	0.004	0.002	-	-	-0.0001	0.0002	-	-			0.073	0.151	-0.001	0.001
SES_cm4	-0.155	0.030	0.005	0.002	-0.011	0.048	-	-	-	-			0.069	0.151	-0.001	0.001

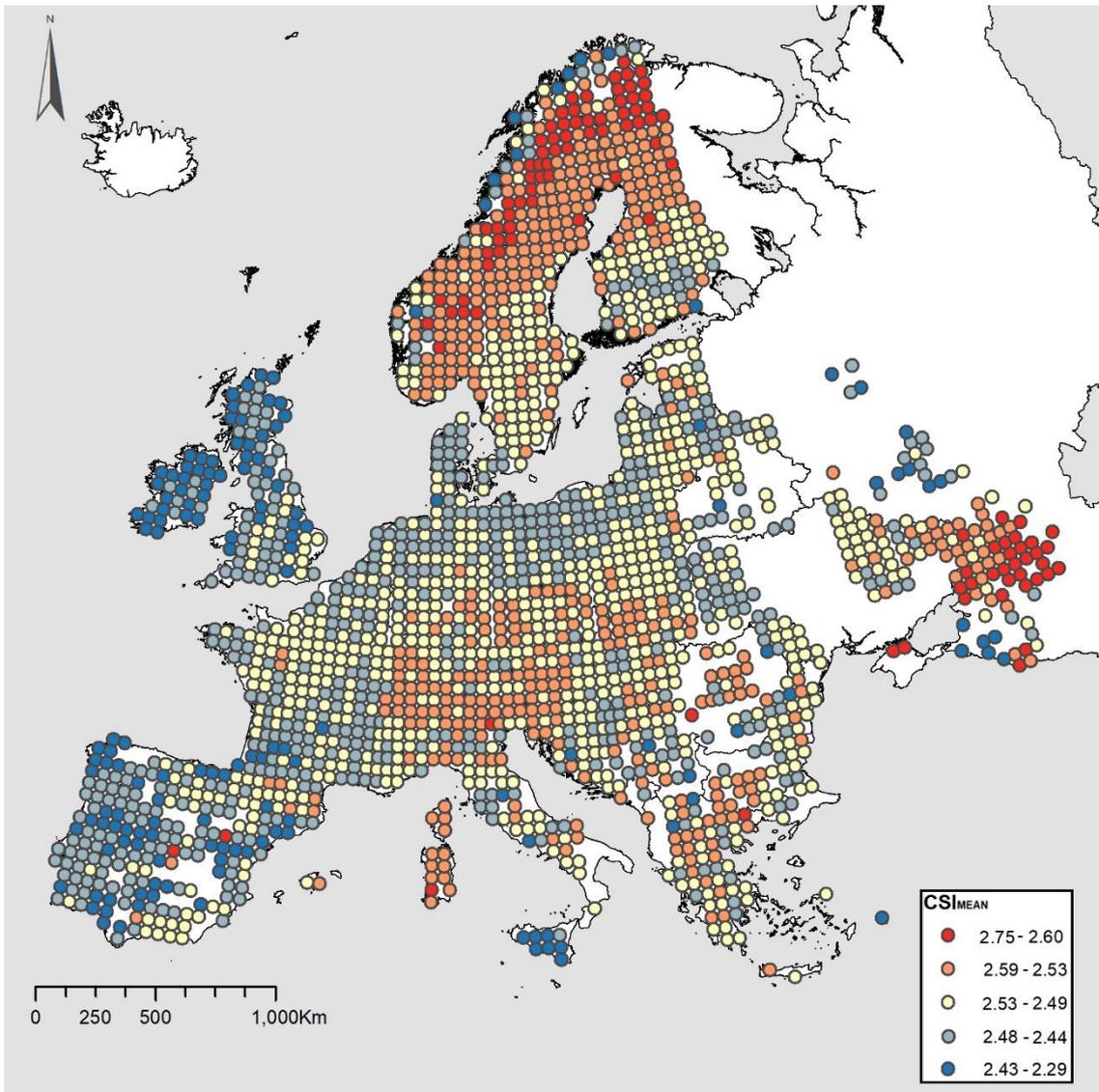
- 676 ⁽¹⁾ Mean altitude in a given mapping square
- 677 ⁽²⁾ Latitude of the centre of a given mapping square
- 678 ⁽³⁾ Longitude of the centre of a given mapping square
- 679 ⁽⁴⁾ Shannon diversity index for the number of habitats available in a given mapping square
- 680 ⁽⁵⁾ Coverage of habitats with anthropogenic origin in a given mapping square

- 681 ⁽⁶⁾ Linear term of mean temperature in a given mapping square
- 682 ⁽⁷⁾ Quadratic term of mean temperature in a given mapping square
- 683 ⁽⁸⁾ Temperature seasonality in a given mapping square
- 684 ⁽⁹⁾ Linear term of mean precipitation in a given mapping square
- 685 ⁽¹⁰⁾ Quadratic term of mean precipitation in a given mapping square
- 686 ⁽¹¹⁾ Precipitation seasonality in a given mapping square

687

688 **Figure 1:** Spatial variation in the specialization indices of bird communities (CSI) consisting of
689 species recorded as breeding in 50 x 50 km in Europe. (a) CSI_{MEAN} – mean of habitat
690 specialization across the species in a given bird community; (b) $SESCSI_{MEAN}$ – standardized
691 effect size of CSI_{MEAN} revealed by controlling for the effect of the species richness; (c) CSI_{SD} –
692 standard deviation of the habitat specialization across the species in a given bird community;
693 (d) $SESCSI_{SD}$ – standardized effect size of CSI_{MEAN} revealed by controlling for the effect of the
694 species richness. See Methods section for more details on definitions of particular variables.

695 a)



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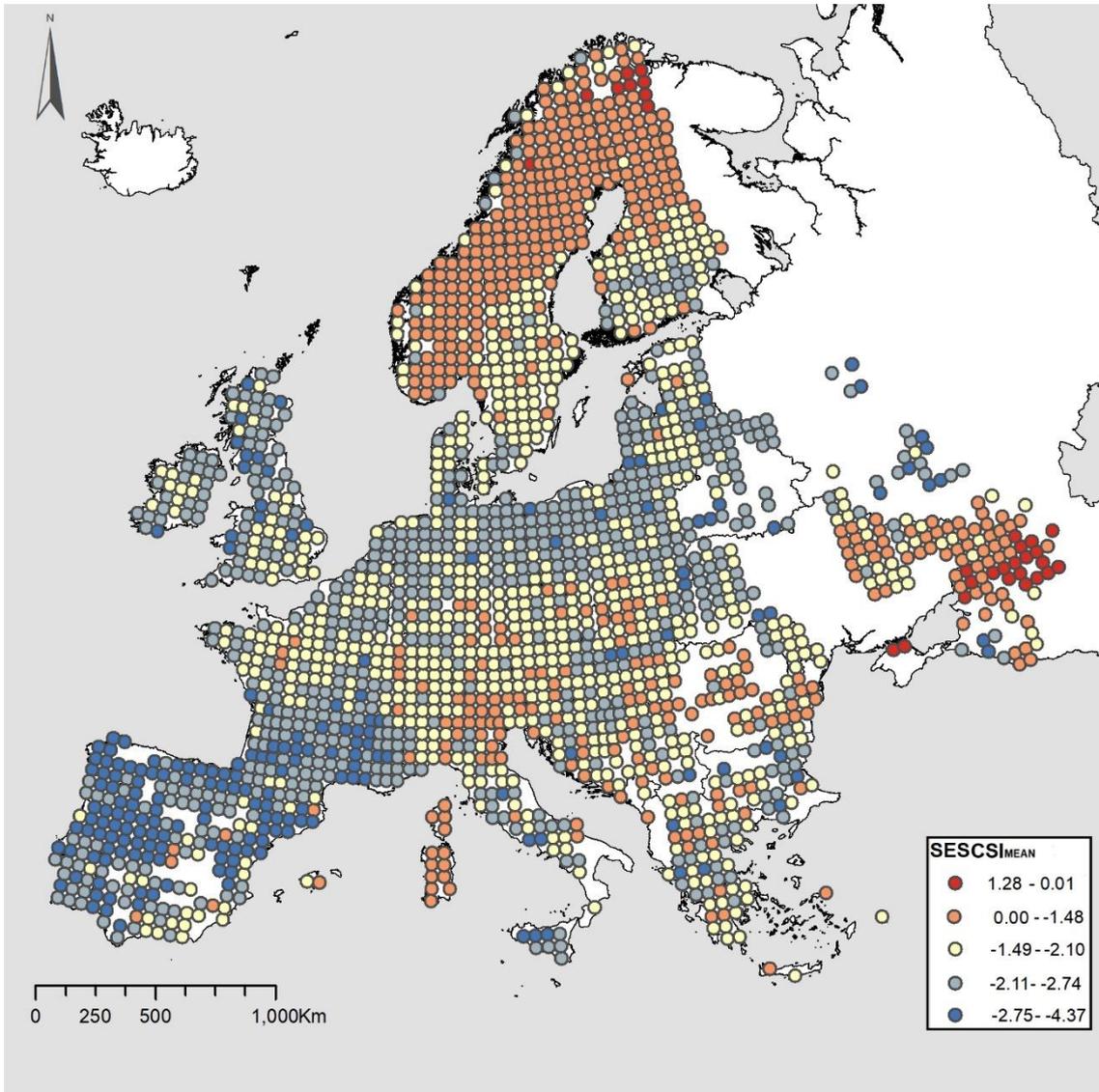
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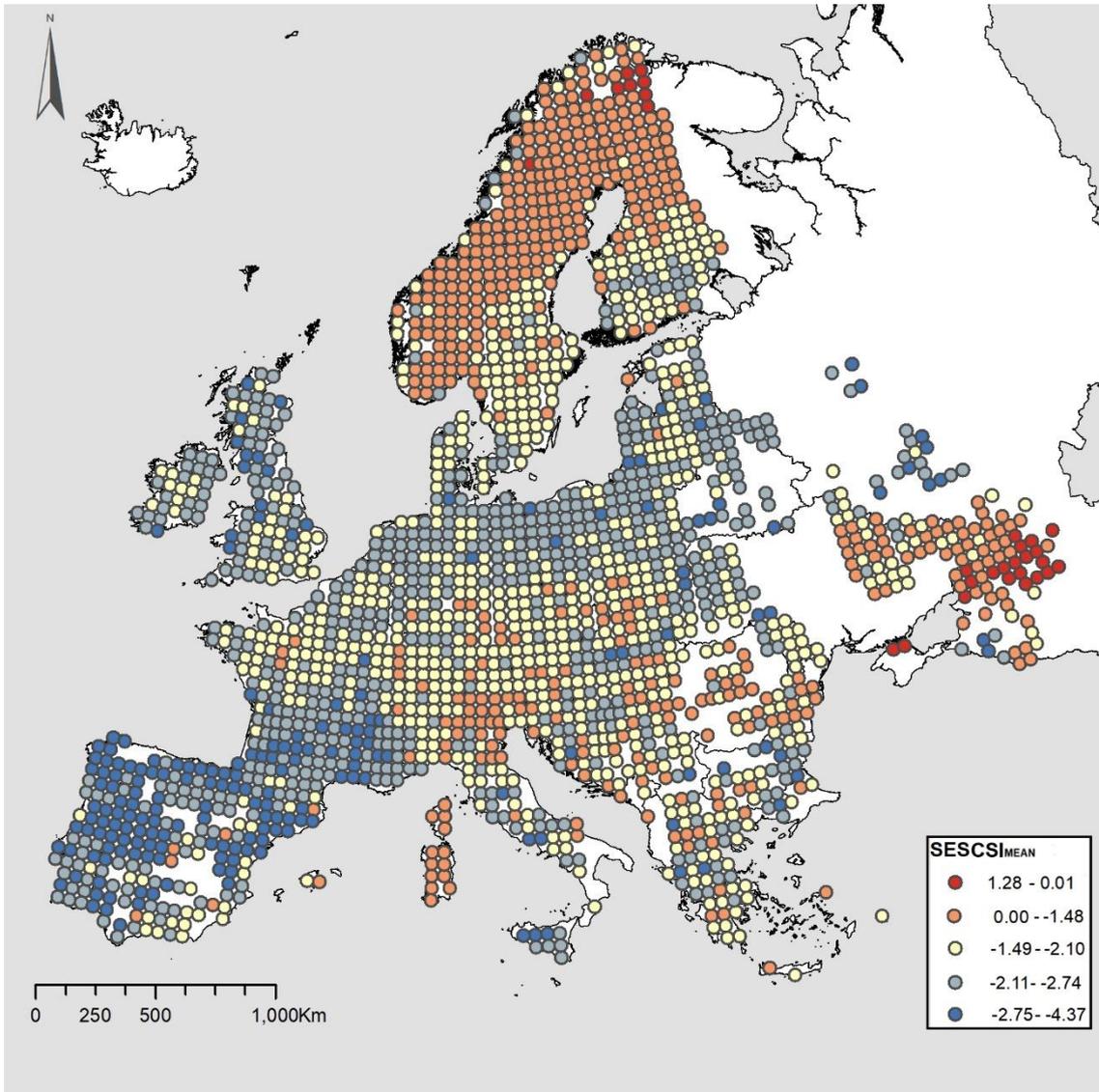
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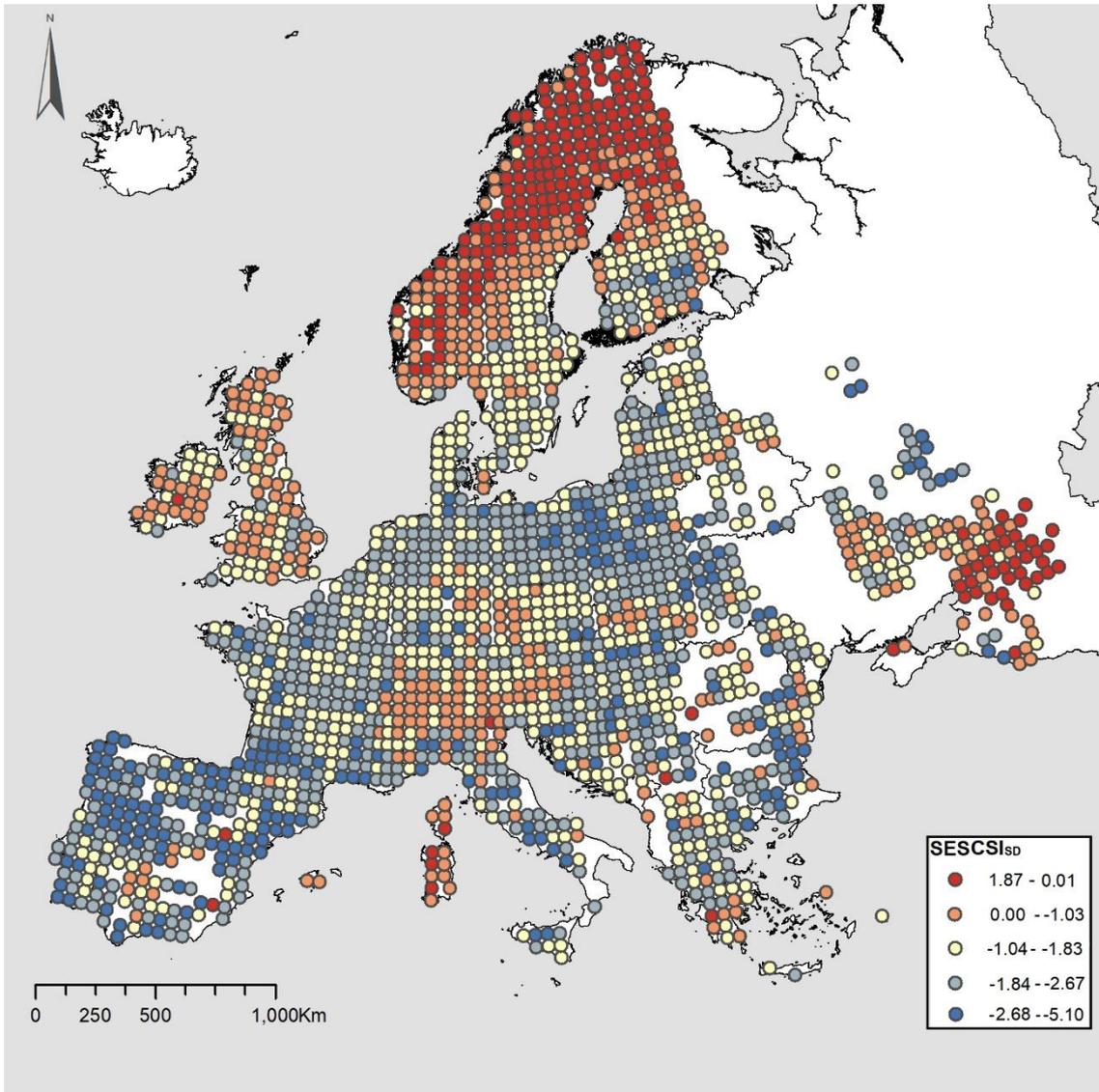
708 c)



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711 d)



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Supplementary material

Table S1a. Pearson correlation coefficients calculated for each pair of climatic variables. See Methods section for definitions of particular geographic variables.

	temp_mean ⁽¹⁾	temp_seas ⁽²⁾	prec_mean ⁽³⁾	prec_seas ⁽⁴⁾
temp_mean	1.000	-0.477	-0.037	0.125
temp_seas	-0.477	1.000	-0.534	0.105
prec_mean	-0.037	-0.534	1.000	-0.184
prec_seas	0.125	0.105	-0.184	1.000

⁽¹⁾ Temperature mean

⁽²⁾ Temperature seasonality

⁽³⁾ Precipitation mean

⁽⁴⁾ Precipitation seasonality

Table S1b. Pearson correlation coefficients calculated for each pair of geographic variables. See Methods section for definitions of particular climatic variables.

	alt_mean ⁽¹⁾	LAT ⁽²⁾	LON ⁽³⁾
alt_mean	1.000	-0.238	-0.221
LAT	-0.238	1.000	0.293
LON	-0.221	0.293	1.000

⁽¹⁾ Mean altitude

⁽²⁾ Latitude

⁽³⁾ Longitude

Table S2. Results of GLs for climatic and geographical models, their degrees of freedom(df), their Akaike information criteria (AIC), the differences among AIC scores(Δ AIC) and the determination coefficient(R^2) expressed as the squared Pearson correlation value among the predicted values and the observed ones. The best performing models (Δ AIC < 2) are in bold.

CSI _{MEAN} Geographic variables	df	AIC	Δ AIC	R^2
CSI_{MEAN} ~alt_mean⁽¹⁾ +LON⁽²⁾	6	-8124.06	0.00	0.244
CSI_{MEAN} ~alt_mean+LAT⁽³⁾ +LON	7	-8123.51	-0.55	0.119
CSI _{MEAN} ~alt_mean	5	-8114.39	-9.68	0.019
CSI _{MEAN} ~alt_mean+LAT	6	-8113.68	-10.38	0.031
CSI _{MEAN} ~LON	5	-8087.94	-36.12	0.187
CSI _{MEAN} ~LAT	5	-8087.73	-36.33	0.088
CSI _{MEAN} ~LAT+LON	6	-8087.51	-36.55	0.085
CSI _{MEAN} Climatic variables	df	AIC	Δ AIC	R^2
CSI_{MEAN} ~temp_mean⁽⁴⁾ +temp2⁽⁵⁾ +prec_mean⁽⁶⁾ +prec_seas⁽⁷⁾	8	-8122.45	0.00	0.181
CSI_{MEAN} ~temp_mean+temp2+prec_mean+prec2⁽⁸⁾ +prec_seas	9	-8121.79	-0.66	0.177
CSI_{MEAN} ~temp_mean+prec_mean+prec2+prec_seas	8	-8121.12	-1.33	0.191
CSI_{MEAN} ~temp_mean+prec_mean+prec_seas	7	-8120.96	-1.49	0.198
CSI _{MEAN} ~temp_mean+temp2+prec_mean	7	-8118.77	-3.68	0.186
CSI _{MEAN} ~temp_mean+prec_mean	6	-8118.62	-3.84	0.207
CSI _{MEAN} ~temp_mean+prec_mean+prec2	7	-8118.48	-3.97	0.198
CSI _{MEAN} ~temp_mean+temp2+prec_mean+prec2	8	-8118.02	-4.43	0.181
CSI _{MEAN} ~temp_mean+prec_mean+prec2+temp_seas ⁽⁹⁾	8	-8117.27	-5.19	0.231
CSI _{MEAN} ~temp_mean+temp2+prec_mean+temp_seas	8	-8117.20	-5.25	0.211

CSI _{MEAN} ~temp_mean+temp2+prec_seas	7	-8117.18	-5.27	0.149
CSI _{MEAN} ~temp_mean+prec_mean+temp_seas	7	-8117.13	-5.32	0.231
CSI _{MEAN} ~temp_mean+temp2+prec_mean+temp_seas	9	-8116.67	-5.79	0.214
CSI _{MEAN} ~temp_mean+prec_seas	6	-8116.18	-6.28	0.172
CSI _{MEAN} ~temp_mean+prec_mean+temp_seas+prec_seas	8	-8115.38	-7.08	0.215
CSI _{MEAN} ~temp_mean+temp_seas	6	-8114.90	-7.55	0.242
CSI _{MEAN} ~temp_mean+temp2+prec_mean+temp_seas+prec_seas	9	-8114.88	-7.57	0.200
CSI _{MEAN} ~temp_mean+prec_mean+prec2+temp_seas+prec_seas	9	-8114.78	-7.68	0.212
CSI _{MEAN} ~temp_mean+temp2+temp_seas	7	-8114.69	-7.77	0.221
CSI _{MEAN} ~temp_mean	5	-8114.58	-7.88	0.175
CSI _{MEAN} ~temp_mean+temp2+prec_mean+prec2+temp_seas+prec_seas	10	-8114.52	-7.93	0.209
CSI _{MEAN} ~temp_mean+temp2	6	-8114.48	-7.98	0.147
CSI _{MEAN} ~temp_mean+temp2+temp_seas+prec_seas	8	-8096.08	-26.37	0.226
CSI _{MEAN} ~temp_mean+temp_seas+prec_seas	7	-8095.45	-27.01	0.244
CSI _{MEAN} ~prec_mean+prec2	6	-8090.03	-32.42	0.020
CSI _{MEAN} ~prec_mean+prec2+prec_seas	7	-8088.25	-34.20	0.020
CSI _{MEAN} ~prec_seas	5	-8086.61	-35.85	0.00003
CSI _{MEAN} ~prec_mean	5	-8086.55	-35.91	0.028
CSI _{MEAN} ~prec_mean+prec_seas	6	-8084.61	-37.85	0.000
CSI _{MEAN} ~prec_mean+prec2+temp_seas	7	-8069.48	-52.97	0.215
CSI _{MEAN} ~temp_seas	5	-8069.31	-53.15	0.214
CSI _{MEAN} ~prec_mean+prec2+temp_seas+prec_seas	8	-8068.08	-54.38	0.207
CSI _{MEAN} ~prec_mean+temp_seas	6	-8067.55	-54.90	0.220
CSI _{MEAN} ~temp_seas+prec_seas	6	-8067.53	-54.92	0.207
CSI _{MEAN} ~prec_mean+temp_seas+prec_seas	7	-8065.84	-56.61	0.213
CSI _{MEDIAN} Geographic variables	df	AIC	ΔAIC	R ²
CSI_{MEDIAN} ~alt_mean+LON	6	-1873.17	0.00	0.161
CSI_{MEDIAN} ~LON	5	-1872.65	-0.52	0.162
CSI_{MEDIAN} ~alt_mean	5	-1872.46	-0.71	0.004
CSI_{MEDIAN} ~alt_mean+LAT+LON	7	-1871.20	-1.98	0.156
CSI _{MEDIAN} ~LAT	5	-1870.79	-2.39	0.035
CSI _{MEDIAN} ~alt_mean+LAT	6	-1870.76	-2.41	0.034
CSI _{MEDIAN} ~LAT+LON	6	-1870.71	-2.47	0.156
CSI _{MEDIAN} Climatic variables	df	AIC	ΔAIC	R ²
CSI_{MEDIAN} ~temp_mean+temp2+prec_mean+temp_seas+prec_seas	9	-1880.73	0.00	0.140
CSI_{MEDIAN} ~temp_mean+temp2+prec_mean+temp_seas	8	-1880.21	-0.52	0.166
CSI_{MEDIAN} ~temp_mean+temp2+temp_seas+prec_seas	8	-1879.26	-1.47	0.150
CSI_{MEDIAN} ~temp_mean+temp2+temp_seas	7	-1879.10	-1.63	0.175
CSI _{MEDIAN} ~temp_mean+temp2+prec_mean+prec2+temp_seas+prec_seas	10	-1878.73	-2.00	0.141
CSI _{MEDIAN} ~temp_mean+temp2+prec_mean+prec2+temp_seas	9	-1878.21	-2.52	0.166
CSI _{MEDIAN} ~temp_mean+temp2+prec_mean+prec_seas	8	-1878.16	-2.57	0.095
CSI _{MEDIAN} ~temp_mean+prec_mean+temp_seas	7	-1877.88	-2.85	0.138
CSI _{MEDIAN} ~temp_mean+temp2+prec_mean	7	-1877.79	-2.94	0.123
CSI _{MEDIAN} ~temp_mean+temp_seas	6	-1877.53	-3.20	0.149
CSI _{MEDIAN} ~temp_mean+prec_mean+temp_seas+prec_seas	8	-1876.98	-3.75	0.117
CSI _{MEDIAN} ~temp_mean+prec_mean+prec_seas	7	-1876.64	-4.09	0.052
CSI _{MEDIAN} ~temp_mean+prec_mean	6	-1876.53	-4.20	0.087
CSI _{MEDIAN} ~temp_mean+temp_seas+prec_seas	7	-1876.53	-4.20	0.127
CSI _{MEDIAN} ~temp_mean+temp2+prec_mean+prec2+prec_seas	9	-1876.25	-4.48	0.095
CSI _{MEDIAN} ~temp_mean+prec_mean+prec2+temp_seas	8	-1875.95	-4.78	0.141
CSI _{MEDIAN} ~temp_mean+temp2+prec_mean+prec2	8	-1875.94	-4.82	0.122
CSI _{MEDIAN} ~temp_mean+prec_mean+prec2+temp_seas+prec_seas	9	-1875.09	-5.64	0.119
CSI _{MEDIAN} ~temp_mean+temp2+prec_seas	7	-1873.50	-7.23	0.042
CSI _{MEDIAN} ~temp_mean+prec_mean+prec2	7	-1873.47	-7.26	0.087

CSI _{MEDIAN} ~temp_mean+prec_mean+prec2+prec_seas	8	-1873.44	-7.32	0.046
CSI _{MEDIAN} ~temp_seas	5	-1873.33	-7.40	0.144
CSI _{MEDIAN} ~temp_mean+prec_seas	6	-1873.28	-7.44	0.023
CSI _{MEDIAN} ~temp_mean	5	-1872.97	-7.76	0.064
CSI _{MEDIAN} ~prec_mean+prec2+temp_seas	7	-1872.97	-7.76	0.143
CSI _{MEDIAN} ~temp_seas+prec_seas	6	-1872.73	-8.00	0.094
CSI _{MEDIAN} ~temp_mean+temp2	6	-1872.29	-8.44	0.093
CSI _{MEDIAN} ~prec_mean+temp_seas	6	-1871.67	-9.06	0.135
CSI _{MEDIAN} ~prec_seas	5	-1871.34	-9.39	0.017
CSI _{MEDIAN} ~prec_mean	5	-1871.28	-9.45	0.020
CSI _{MEDIAN} ~prec_mean+temp_seas+prec_seas	7	-1871.04	-9.68	0.087
CSI _{MEDIAN} ~prec_mean+prec2	6	-1870.97	-9.76	0.019
CSI _{MEDIAN} ~prec_mean+prec_seas	6	-1870.51	-10.22	0.0001
CSI _{MEDIAN} ~prec_mean+prec2+temp_seas+prec_seas	8	-1869.45	-11.28	0.092
CSI _{MEDIAN} ~prec_mean+prec2+prec_seas	7	-1868.70	-12.03	0.0004
CSI _{SD} Geographic variables	df	AIC	ΔAIC	R ²
CSI_{SD} ~alt_mean+LAT+LON	7	-9861.90	0.00	0.400
CSI_{SD} ~alt_mean+LAT	6	-9861.73	-0.16	0.388
CSI _{SD} ~alt_mean	5	-9853.02	-8.87	0.020
CSI _{SD} ~alt_mean+LON	6	-9852.92	-8.98	0.109
CSI _{SD} ~LAT+LON	6	-9807.07	-54.82	0.317
CSI _{SD} ~LAT	5	-9806.82	-55.08	0.313
CSI _{SD} ~LON	5	-9798.11	-63.79	0.068
CSI _{SD} Climatic variables	df	AIC	ΔAIC	R ²
CSI_{SD} ~temp_mean	5	-9857.90	0.00	0.379
CSI_{SD} ~temp_mean+prec_mean	6	-9857.59	-0.31	0.374
CSI_{SD} ~temp_mean+temp2	6	-9857.01	-0.89	0.403
CSI_{SD} ~temp_mean+temp2+prec_mean	7	-9856.53	-1.37	0.395
CSI_{SD} ~temp_mean+prec_seas	6	-9856.36	-1.54	0.379
CSI_{SD} ~temp_mean+prec_mean+prec_seas	7	-9856.18	-1.72	0.372
CSI _{SD} ~temp_mean+temp_seas	6	-9855.90	-2.00	0.379
CSI _{SD} ~temp_mean+prec_mean+prec2	7	-9855.88	-2.02	0.394
CSI _{SD} ~temp_mean+prec_mean+temp_seas	7	-9855.82	-2.08	0.374
CSI _{SD} ~temp_mean+temp2+prec_seas	7	-9855.22	-2.68	0.007
CSI _{SD} ~temp_mean+temp2+temp_seas	7	-9855.01	-2.89	0.399
CSI _{SD} ~temp_mean+temp2+prec_mean+prec2	8	-9854.98	-2.92	0.395
CSI _{SD} ~temp_mean+temp2+prec_mean+prec_seas	8	-9854.85	-3.06	0.391
CSI _{SD} ~temp_mean+temp2+prec_mean+temp_seas	8	-9854.72	-3.18	0.399
CSI _{SD} ~temp_mean+prec_mean+prec2+prec_seas	8	-9854.51	-3.40	0.371
CSI _{SD} ~temp_mean+temp_seas+prec_seas	7	-9854.37	-3.53	0.379
CSI _{SD} ~temp_mean+prec_mean+temp_seas+prec_seas	8	-9854.36	-3.54	0.373
CSI _{SD} ~temp_mean+prec_mean+prec2+temp_seas	8	-9854.05	-3.85	0.394
CSI _{SD} ~temp_mean+temp2+prec_mean+prec2+prec_seas	9	-9853.31	-4.59	0.389
CSI _{SD} ~temp_mean+temp2+temp_seas+prec_seas	8	-9853.23	-4.67	0.003
CSI _{SD} ~temp_mean+temp2+prec_mean+prec2+temp_seas	9	-9853.10	-4.80	0.370
CSI _{SD} ~temp_mean+temp2+prec_mean+temp_seas+prec_seas	9	-9853.01	-4.89	0.371
CSI _{SD} ~temp_mean+prec_mean+prec2+temp_seas+prec_seas	9	-9852.63	-5.27	0.389
CSI _{SD} ~temp_mean+temp2+prec_mean+prec2+temp_seas+prec_seas	10	-9851.41		
			-6.49	0.402
CSI _{SD} ~prec_mean+prec2	6	-9802.47	-55.43	0.004
CSI _{SD} ~prec_mean+prec2+prec_seas	7	-9801.59	-56.32	0.371
CSI _{SD} ~prec_mean+prec2+temp_seas	7	-9800.48	-57.42	0.001
CSI _{SD} ~prec_mean+prec2+temp_seas+prec_seas	8	-9799.60	-58.30	0.390
CSI _{SD} ~prec_mean	5	-9799.53	-58.37	0.0005
CSI _{SD} ~prec_mean+prec_seas	6	-9799.24	-58.66	0.002
CSI _{SD} ~prec_seas	5	-9797.73	-60.17	0.003
CSI _{SD} ~prec_mean+temp_seas	6	-9797.59	-60.32	0.004

CSl _{SD} ~prec_mean+temp_seas+prec_seas	7	-9797.30	-60.60	0.001
CSl _{SD} ~temp_seas	5	-9796.55	-61.35	0.089

- (1) Mean altitude
- (2) Longitude
- (3) Latitude
- (4) Temperature mean
- (5) Squared temperature mean
- (6) Precipitation mean
- (7) Precipitation seasonality
- (8) Squared precipitation seasonality
- (9) Temperature mean

Figure 1a
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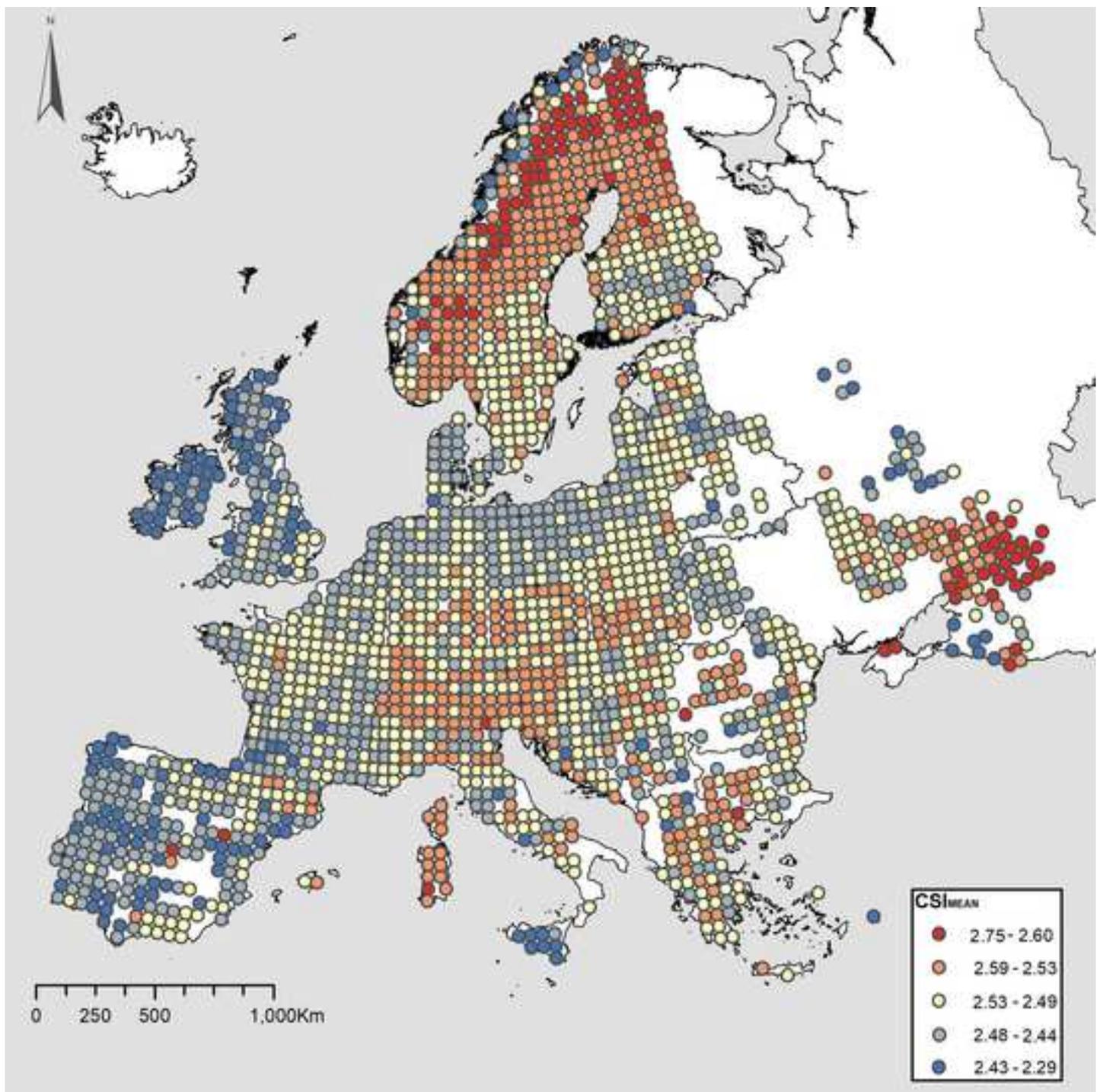


Figure 1b
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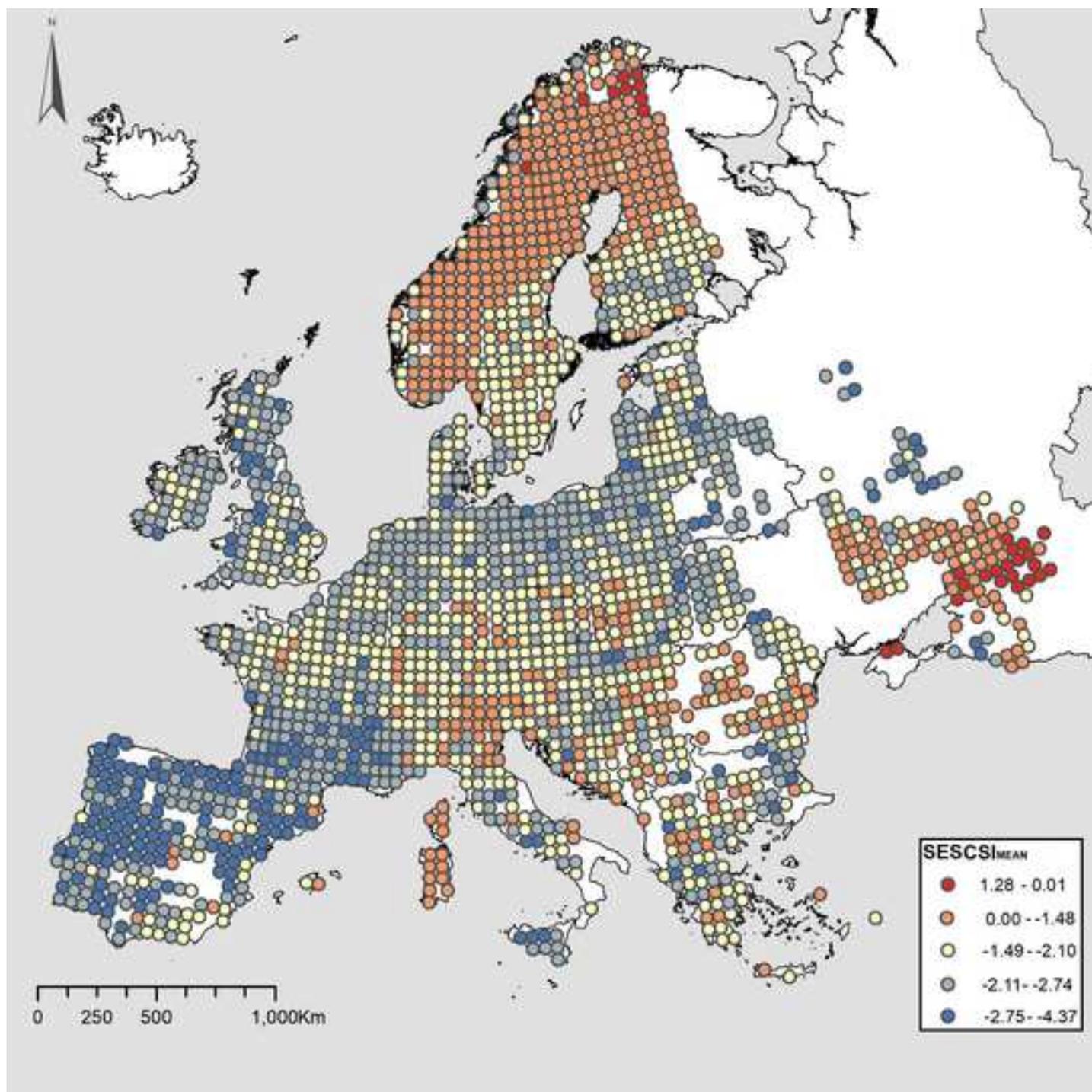


Figure 1c
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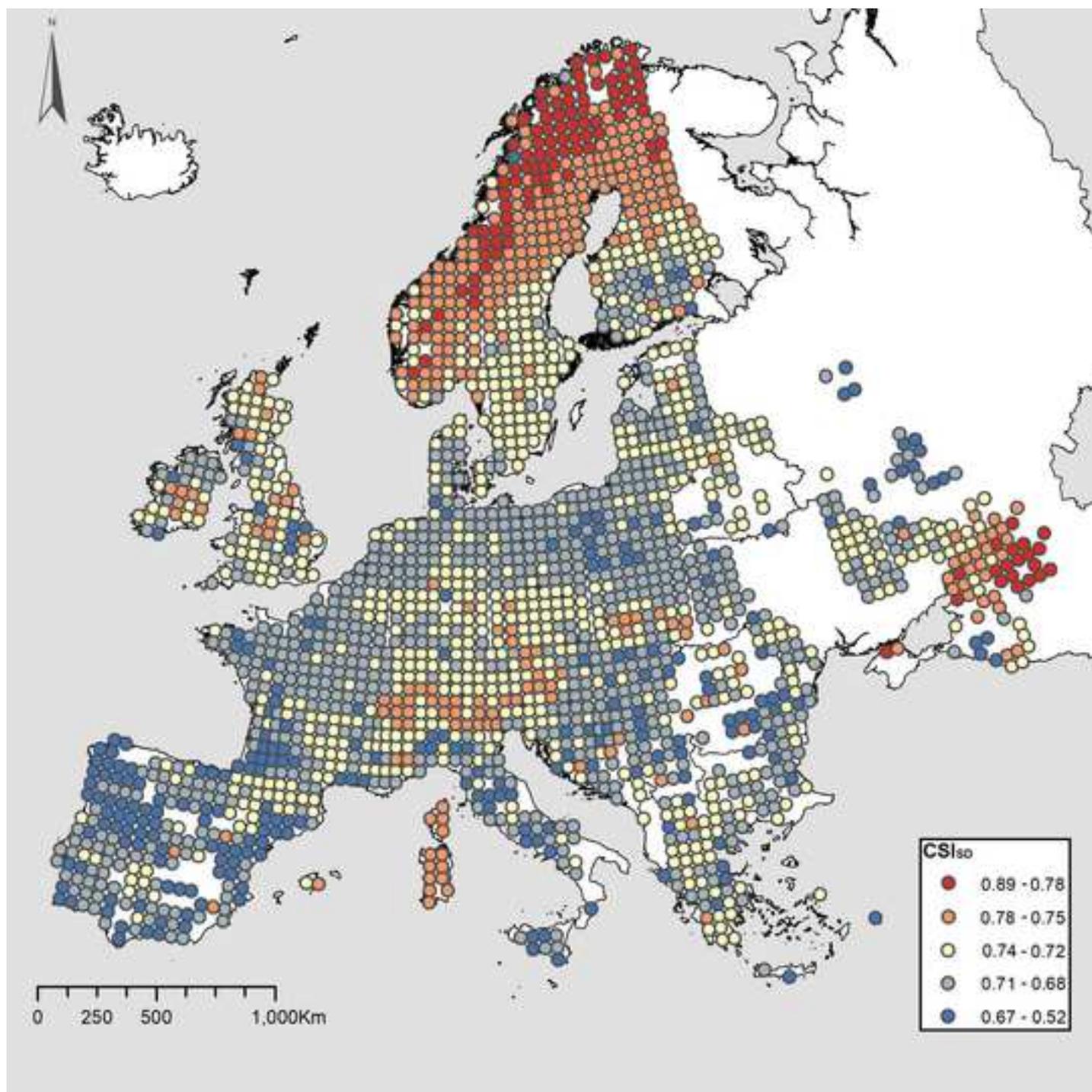
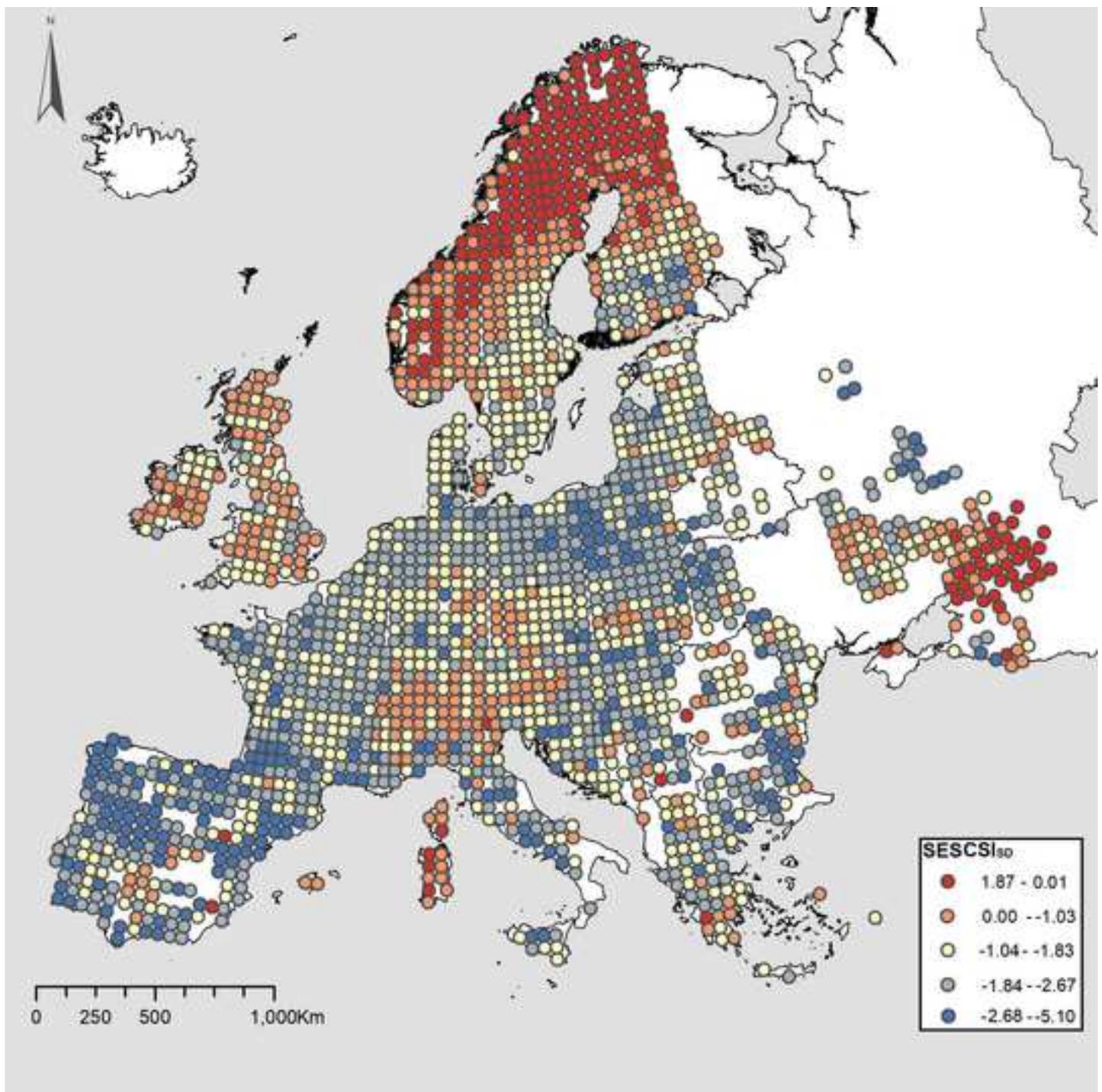


Figure 1d
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Manuscript II

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Continent-wide test of the efficiency of the European union's conservation legislation in delivering population benefits for bird species.

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1 **Continent-wide test of the efficiency of the European union's conservation legislation in**
2 **delivering population benefits for bird species**

3

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5

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9

10 **Abstract**

11 Birds are among the most important organisms for indicating the state of environmental health
12 and their population changes may be thus informative for assessments of country-level
13 conservation tools. One such tool applied in the European Union (EU) is the Birds Directive
14 which (together with general protection of all bird species) lists a number of species under its
15 Annex I and these species enjoy specific protection conditions. Although some previous
16 studies found indications of the efficiency of the Annex I in delivering benefits for the listed
17 species, the assessments were either confined to the so called old member states (i.e.
18 countries entered EU before 2004) or did not include countries outside EU as a suitable
19 control group. Therefore, it remains unclear whether this tool is efficient also in the new EU-
20 member states (i.e. countries entered EU from 2004 onwards). For this purpose, we used
21 publicly available information source and assembled a dataset providing country-level
22 population trends of 252 European breeding bird species estimated for the time period 2001-
23 2012 in 33 European countries containing old member states, new member states and non-
24 member states. We predicted that if efficient, then listing the species under Annex I would
25 result in significantly positive population trends of the listed species in EU countries
26 irrespective to the time of their entrance, while no such pattern should be observed in non-
27 EU countries. We tested this prediction using linear mixed effect models controlling for the
28 effects of 11 species' traits reflecting the influence of other factors (e.g. climate change, land
29 cover change, proximity to range edges) on trends and including the species and country
30 identifiers as random effects. We found that the listing under the Annex I had significantly

31 positive effect on bird trends in both old and new member states, whereas no such effect was
32 observed in the non-member states. Although the positive influence of listing was larger in the
33 old and than in the new member states, the difference was not statistically significant. Our
34 results imply that the Annex I of the Birds Directive is an important tool for bird conservation
35 in Europe and that its positive influence on bird populations is detectable even in the new EU
36 members entering EU relatively recently. As birds are often used as indicators also for other
37 groups of organisms, these results suggest that not only birds may benefit from EU's
38 conservation legislation but comprehensive assessments are needed.

39

40 **Keywords:** birds, legal protection, Birds Directive, Annex I, traits, population trends

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42 **1. Introduction**

43 Due to their generally large body size, diurnal activity and popularity among citizen scientists
44 (Jiguet et al., 2012; Morelli et al., 2014), birds play a major role in indicating efficiency of
45 conservation actions (Butchart et al., 2010). For instance, annual changes in population size of
46 farmland birds were used to develop the Farmland Bird Index (Gregory et al., 2005), which is
47 included among official indicators of environmental health in the European Union (EU). As
48 indicators, populations of bird species mirror influences of factors acting at larger spatial
49 scales (Gregory and Van Strien, 2010) and their population changes may be thus informative
50 for assessment of country-level conservation tools.

51 One of such conservation tools applied at the country level is legal protection of
52 endangered species (McCarthy et al., 2012). By that means, species with unfavourable
53 population status may be listed as protected in a given country and specific regulations (e.g.
54 prohibition of their hunting and disturbance of individuals, restrictions to alteration of their
55 habitats, direct support of impoverished populations) are agreed as the measures aiming to
56 improve their populations (Vorisek et al., 2008). If efficient, population trends of species
57 being listed as legally protected should be more positive than the trends of the species for
58 which no such tool was developed (Koleček et al., 2014), although a time lag may exist
59 between the time of listing and detectable population improvement (Male and Bean, 2005).

60 In EU, legal protection of birds is applied through the Birds Directive which states
61 general conditions for protection of all bird species on the territory of EU-member countries
62 (Council Directive 79/409/EC on the conservation of wild birds). In addition, the Birds
63 Directive also lists a number of species under its Annex I and these species enjoy specific
64 protection conditions, most notably manifested by establishment of Special Protected Areas
65 (SPAs) conserving key sites for these species in individual countries (Donald et al., 2007).
66 Such a combination of species- and area-focused protection may be a particularly powerful
67 tool for conserving of animal populations (Sutherland, 2000) and, for that reason, it deserved
68 high attention from the side of researchers testing its efficiency (e.g. Donald et al., 2007;
69 Pellisier et al., 2013; Sanderson et al., 2016; Gamero et al., 2017). Specifically, they tested
70 whether species listed under Annex I really benefited from their listing, i.e. whether it resulted
71 in significant improvement of their population status.

72 These previous studies found that the listing of the species under the Annex I of the
73 Birds Directive contributes significantly to their population increase (Donald et al., 2007;
74 Gamero et al., 2017) and that the population improvement was larger with the longer the time

75 since listing (Sanderson et al., 2016). However, the previous tests also showed a great
76 difference between the old and new EU-member states (i.e. the states that entered EU before
77 2004 and the states entered from 2004 onwards, respectively) when the significant
78 improvement was found only in the old members, but not in the new members (Sanderson et
79 al., 2016). This finding thus poses an important question, whether the efficiency of this
80 legislative tool for bird conservation is confined specifically to some selected countries being
81 part of European democratic structures for considerably long time, while it may fail to provide
82 conservation benefits in the new member states which underwent different historical
83 development, as some studies already showed that these historical differences mirror in bird
84 population changes (Reif et al., 2011; Koleček et al. 2015).

85 To fill this knowledge gap, our study, for the first time, assembled publicly available
86 data on bird population trends from 2000 to 2012 in 33 European countries of a continent-
87 wide coverage including the states in the Eastern part of Europe (e.g. Russia, Belarus and
88 Ukraine) whose bird populations have almost been neglected up to now. This set of countries
89 includes (i) the states entering EU before 2004 (i.e. the ‘old member states’ or EU-15), (ii) the
90 states entering EU from 2004 or onwards (the ‘new member states’) and (iii) the states being
91 non-members of EU. Such a design provides a strong test for the impact of listing the species
92 under the Annex I assuming that the population trends estimated over the focal time period
93 were affected by the entrance of a given country into the EU.

94 In this context, we tested two predictions. (i) If this legislative tool was efficient, than
95 listing the species under Annex I would result in significantly positive population trends of
96 the listed species in the EU member states irrespective to the time of their entrance, while no
97 such pattern should be observed in the non-member states. (ii) If the time since listing matters,
98 we predict that the population trends of the listed species should be more positive in the old
99 member states than in the new member states.

100 In addition to the effect of legal protection, interspecific variability in population
101 trends is influenced by various other factors including land use change, climate change or
102 proximity to range edge (e.g. Devictor et al., 2012; Cuervo and Møller, 2013; Diaz et al.,
103 2015). Their influence may be quantified by the relationships between the trends and species-
104 specific traits reflecting the effects of particular environmental filters thereby a group of
105 species sharing a given trait should exhibit similar population trends (Webb et al., 2010).
106 Therefore, we considered the species’ traits recently recognized by a review of Reif (2013) as
107 important predictors of bird population trends and accounted for their effects in the analysis
108 (see Table 1 for the expected relationships and their justifications).

109

110 **2. Materials and Methods**

111 **2.1 Population trends**

112 We focused on 252 bird species breeding in Europe that were previously analysed for
113 potential range shifts by Koschová et al. (2014), see Supplementary Table S.1. We excerpted
114 their national population trends for 33 European countries (Supplementary Table S.2) over the
115 time period from 2001 to 2012 from the European Red List of Birds (BirdLife International
116 2015). Because not all species breed in every country, we finally obtained the dataset with
117 4459 species-country combinations. These trends were expressed as relative change over the
118 focal time period in per cent when negative percentage values quantified population declines,
119 whereas positive percentage values quantified population increases (BirdLife International
120 2015). When the trend was provided as a range of the maximum and minimum estimates (e.g.
121 decline from -30% to -60%), we calculated the mean trend from these values (i.e. -45%).
122 Quantification of population change as percentage raises concerns about comparability of the
123 magnitude of change between declining and increasing species since doubling the population
124 size equals to the increase by 200%, while reducing the population to one half equals to the
125 decline by 50%. These incomparable values make inference from interspecific comparisons of
126 such trends impossible (Lemoine et al. 2007). Therefore, we followed Lemoine et al. (2007)
127 and recalculated the population change using the expression $(N_{t+1} - N_t) / ((N_{t+1} + N_t) / 2)$,
128 when N_t is population size in the time t (i.e. 2000) and N_{t+1} is population size in the time $t+1$
129 (i.e. 2012). N_t was set to 100% and N_{t+1} was the relative population change proportional to the
130 original trend value (e.g. for the population decline by -20%, the $N_{t+1} = 80\%$; for the
131 population increase by 20%, the $N_{t+1} = 120\%$). By that means, we obtained an index of
132 population change ranging from -2 to 2, when negative values correspond to population
133 declines, positive values to population increases and zero to no change. Values of this index
134 are comparable for population declines and increase (for instance, doubling the population
135 size equals to the index value of 0.67, while reducing the population size to one half equals to
136 the index value of -0.67). This population index was thus taken as a response variable for
137 further analysis.

138

139 **2.2 Annex I species and country classification**

140 To focus on testing the efficiency of listing the species under the Annex I of the Birds
141 Directive, we discriminated the species being listed (1) from those being unlisted (0)
142 according to the information in BirdLife International (2015), see Supplementary Table S.1.

143 Since we expected country-specific effects of being listed on species' population trend
144 varying according to the time a given country entered EU, we classified the countries as the
145 old member states (i.e. countries which entered EU before 2004), the new member states (i.e.
146 the countries which entered EU from 2004 onwards) and non-member states (i.e. the countries
147 which did not access EU). This classification was expressed as a three-level factor 'country
148 status' (Supplementary Table S.2) and was used as a country-specific explanatory variable for
149 further analysis.

150

151 **2.3 Species' traits**

152 For each species, we collected information about following 11 traits (see Table 1 for summary
153 information and Supplementary Table S.1 for trait values for each species).

154 Habitat use was expressed using four variables taken from Koschová et al. (2014).
155 Each species was assigned to one of more habitats along a gradient from forest interior
156 (position of 1) to open treeless landscape (position of 7) assessed in Böhning-Gaese and
157 Oberrath (2003). From this assignment (i) habitat niche position was calculated a mean value
158 of across habitats used by a given species (Reif et al., 2011). As a complement to the habitat
159 niche position, (ii) habitat niche breadth was expressed as a difference between the values of
160 habitats used by a given species at the extremes of the gradient mentioned above (Reif et al.,
161 2011). Classification of species' position along the (iii) humidity gradient discriminated
162 species of non-humid (1), wetland (2) and water habitats (3) assessed in Böhning-Gaese and
163 Oberrath (2003). Finally, we assessed (iv) species' relation to built-up areas discriminating
164 species breeding in such areas (1) and species not breeding in these areas (0) using
165 information in Cramp (1977-1994).

166 The effects of climate change were expressed using two variables taken from
167 Koschová et al. (2014) based on characteristics of European breeding ranges of particular
168 species: (i) latitude of the mean range centre and (ii) magnitude of potential range shift.
169 Koschová et al. (2014) used maps from Huntley et al. (2007) for their inference. These maps
170 were constructed using bioclimatic modelling of the breeding bird distribution in Europe
171 using the information from Hagemeyer and Blair (1997) on current breeding ranges of
172 particular species. Huntley et al. (2007) first modelled the present climatic range of every
173 species and the revealed relationship between species' breeding distribution and climatic
174 variables was applied in the next step to predict the future climatic ranges of bird species
175 under the climatic projection for the period 2070 – 2099 (IPCC 2001). Using these data from
176 Huntley et al. (2007), Koschová et al. (2014) calculated the mean centre (mean longitude and

177 mean latitude), for both the current and the predicted future climatic range of every species.
178 The potential range shift of a given species was the difference between these mean centres in
179 kilometres (Koschová et al., 2014).

180 We also considered five more ecological traits to test their potential relationships to
181 bird population trends: (i) diet niche breadth was based on a classification of species into three
182 groups obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and
183 insectivorous/carnivorous (2) and omnivorous (3) in Koschová et al. (2014); (ii) migration
184 strategy was based on classification of species as residents (1), short-distance migrants (2),
185 and long-distance migrants (3) in Koschová et al. (2014); (iii) marginality of the position of
186 species' European breeding ranges in respect to their Eurasian breeding ranges (expressing
187 the marginality of the European distributions) was calculated as a distance between mid-
188 longitudes of Eurasian and European ranges based on the analysis of range maps from
189 BirdLife International (2016) - the larger the difference, the more marginal population is
190 represented by our European data for a given species; (iv) life history strategy was taken from
191 Koschová et al. (2014) who expressed position of each species along a slow-fast life history
192 axis revealed by principal component analysis of six life-history traits: body mass, egg mass,
193 number of broods per year, laying date (julian date of the beginning of laying in the first
194 breeding), clutch size and length of incubation; (v) nest location was based on data from
195 Koleček et al. (2014) who recognized species breeding on the ground or close to (0), species
196 breeding in intermediate heights such as shrubs and small trees (1) and species breeding in
197 high trees (2).

198 We tested for possible collinearity among the trait variables by calculating the Pearson
199 correlation coefficients for each pair of variables (Supplementary Table S.3) and found that
200 all correlations were below 0.7 which is considered as a level when the issue of collinearity
201 arises (Dorman et al., 2013).

202

203 **2.3 Data analysis**

204 We used linear mixed effects modelling framework within the R package 'nlme' (Pinheiro et
205 al., 2010) to test the influence of listing under the Annex I of the Birds Directive on
206 population trends of European birds. We proceeded in several steps following the approach of
207 Koleček et al. (2014) who performed a similar analyses focused on the efficiency of the
208 national legislation for protection of bird species in ten Eastern European countries. First, we
209 selected the species' traits with the largest continent-level influence on bird population trends
210 to control for their possible confounding effects on population trends potentially masking the

211 effect of the Annex I of the Birds Directive. For this purpose, we run the models with the main
212 effects of particular species' traits and the interaction between the potential range shift and the
213 latitude of the mean range centre to account for variability in climate change impacts on
214 species across latitudes (see Koschová and Reif, 2014). We performed model selection based
215 on the information-theoretic approach to assess the relative importance of all possible
216 combinations of the predictor variables (Burnham and Anderson, 2002). Using Akaike
217 Information Criterion corrected for small sample sizes (AIC_c) we assessed relative
218 performance of every combination of predictor variables within the R-package 'MuMIn'
219 (Barton, 2015) and selected the models with ΔAIC_c less than two as the best performing
220 models (Burnham and Anderson, 2002). Second, we took the variables present in these best
221 performing models and composed a final model where we added the variable 'listing the
222 species under the Annex I', the variable 'country status' and their interaction. This interaction
223 tests for the differences in the effect of listing the species under the Annex I among the old
224 member states, the new member states and the non-member states. We assessed the
225 importance of this interaction using the likelihood ratio test. To take the replicates at the
226 species- and country-level into account, we included the variable 'species' nested within the
227 variable 'country' as random effects into all models following the approach of Gamero et al.
228 (2017). All analyses were performed in R 2.12.0 (R Development Core Team, 2010).

229

230 **3. Results**

231 In the analysis selecting the species' traits according to the strength of their relationships to
232 population trends, three models were assessed as the best performing ones by the information-
233 theoretic approach with their ΔAIC_c lower than two (Table 2). All these models contained
234 nest location and life history strategy, two models contained species' position along the
235 humidity gradient and one model contained habitat niche breadth (Table 2).

236 In the next step, we combined these variables into a single model, where we also
237 included listing the species' under the Annex I of the Birds Directive, country status and their
238 interaction (Table 3). This interaction was found as significantly improving the model fit
239 according to the likelihood ratio test (likelihood ratio between the models with and without
240 this interaction = 9.90, $P = 0.007$), so we used this model as the final one for the inference.

241 The parameter estimates of this final model (Table 3) showed that listing the species
242 under the Annex I resulted in significantly increasing population trends and that this
243 improvement of populations in the listed species was highest in the old member states (Fig.
244 1). For the new member states, the positive effect of listing the species under the Annex I

245 was slightly lower but still significant (Fig. 1), while no significant relationship between
246 population trend and listing under the Annex I was observed in the non-member states (Fig.
247 1).

248 All trait variables included into the final model were significantly related to bird
249 population trends (Table 3). More positive trends were found for species having broader
250 habitat niches, breeding in more humid habitats, having slower life history strategies and
251 breeding higher above ground (Table 3).

252

253 **4. Discussion**

254 Our results showed that listing the species under the Annex I of the EU's Birds Directive
255 resulted in their more positive population trends compared to the non-listed species.

256 Importantly, this positive effect of legal protection was not confined only to the so called old
257 member states of EU (i.e. the countries which entered EU before 2004) reported by Donald et
258 al. (2007) and Sanderson et al. (2016), but were also observed for the new member states, i.e.
259 the countries entering EU from 2004 onwards. Our study thus for the first time showed
260 significant conservation benefits delivered by listing the species' under the Annex I applies to
261 the whole EU. These positive effects of EU's conservation legislation contrast with their
262 absence in the countries which are not EU members.

263 What is the mechanism mediating the population benefits for birds being listed under
264 the Annex I of the Birds Directive in EU countries? We suggest three important drivers of this
265 success: (i) setting the EU-wide (i.e. supranational) conservation priorities, (ii) scientific basis
266 of species selection and (iii) establishment of protected areas for the species. Concerning the
267 first point, it is important to realize that the bird species' ranges are usually much larger than
268 the areas of individual countries (Gaston, 2003) and that species' populations are connected
269 by dispersal or migration among countries (Gilroy et al., 2016). Therefore, protection of a
270 species in one country may be effectively compromised by its absence for the same species in
271 a neighbouring state (Pouzols et al., 2014). The Birds Directive overcomes this problem by
272 protecting the species' populations from the EU-wide perspective. By that means, the species
273 recognized as deserving protection in EU are listed under the Annex I in all member states
274 which results in protection of significant parts of their European (or even global) populations.
275 This large-scale protection may then translate in population increase in all countries involved.

276 Second, species are selected for Annex I within a sophisticated system of scientific
277 criteria. They focus on species' population status in EU and on the proportion of EU's
278 population shared by individual countries (Donald et al., 2007). By that means, a country

279 protects the species of the EU-wide interest whose significant part of population occurs in that
280 country (Donald et al., 2007). This guarantees efficient spending of inevitably limited
281 conservation resources when the greatest emphasis is targeted to areas hosting the population
282 strongholds of the focal species, whereas marginal areas where a given species occurs rarely
283 are neglected. This approach is in accord with the current knowledge of population ecology of
284 animals in space showing that source populations are crucial for species' persistence, while
285 sinks are of minor importance (Pulliam, 1988). Third, although the sole effect of listing as
286 legally protected may be beneficial for the target species in terms of the reduction of the direct
287 persecution (Koleček et al., 2014), the species listed under the Annex I enjoy particular
288 benefits from establishment of protected areas, i.e. SPAs, aimed specifically to satisfy the local
289 needs of these species (Donald et al., 2007). Designation of individual SPAs is performed at
290 the national level by local experts based on scientific criteria to cover the key localities for
291 species' population in a given country (Donald et al., 2007). Once again, this approach
292 ensures that the focal species are protected at their most important sites of occurrence from
293 the EU-wide perspective.

294 Our study supports the findings of Sanderson et al. (2016) about longitudinal increase
295 of positive effect of listing the species under the Annex I. We found that the listed species had
296 the most positive trends in the old member states and somewhat less positive in the new
297 member states, but the difference between old and new member states was not significant. As
298 the usual time lag between listing the species as protected and detection of improvement of its
299 population status is between 5 and 10 years (Male and Been, 2005; Sanderson et al., 2016),
300 we suggest that this result broadly coincides with the start of EU-membership in the majority
301 of the new member states in our sample which took place in 2004. Therefore, the time period
302 of 2000-2012 used for the estimation of the abundance trends most likely mirrors population
303 improvement of the listed species in new member states after their EU entrance and the
304 pattern was probably not caused by some other factors. Our results thus imply that even if the
305 new member states underwent historical development largely different from the old member
306 states (Reif et al., 2011), implementation of the EU's conservation legislation was successful
307 in these countries and resulted in conservation benefits for the Annex I species. We can
308 predict that the population improvement of these species in the new member states will be
309 even stronger in the future with the longer time elapsed since their EU entrance. Another
310 concern about the observed positive influence of EU's conservation legislation may be that
311 the bird populations in the new member states may improve even without entering EU due to
312 generally better environmental conditions in the Eastern European countries, which are

313 believed as strongholds of European biodiversity (Sutcliffe et al., 2015). However, a great
314 contrast in the statistical effect of the species' listing between the new member states and non-
315 members indicates that this mechanism is hardly applicable. In addition, we did not observe
316 any differences in mean bird population trends (after controlling the effect of listing) among
317 old member states, new member states and non-members implying that presumably better
318 environmental conditions in the Eastern Europe either recently deteriorated or did not mirror
319 in positive bird population trends.

320 Recognition of species' threat based on an unfavourable population status is a usual
321 first step before including a given species among those that are legally protected (Sutherland,
322 2000). For this purpose, the IUCN Red List is the most widely used and respected tool under
323 which the species are assessed based on purely biological criteria concerning population and
324 geographic range size characteristics (Mace et al., 2008). However, listing the species under
325 the IUCN Red List (either global or regional) does not guarantee that this species will be
326 inevitably the subject of a conservation management including its listing among legally
327 protected species. Indeed, an assessment of the rates of species' movement between particular
328 IUCN Red List categories among assessments performed at different time points indicates
329 that only the most threatened species move more often towards downlisting than towards
330 uplisting in the subsequent assessment, while the less threatened species are more often
331 uplisted (Brooke et al., 2008). This is in a clear contrast to our finding that the species listed
332 as protected in EU have population trends more positive than the unprotected species. It thus
333 seems that the way from recognition of a species as threatened to a detectable improvement of
334 its population status is quite long and the success at the end is uncertain. Therefore, we
335 suggest that the links between threat assessments and listing the species as protected should
336 be closer and the EU's conservation legislation may be inspirational in this respect.

337 Our results add to the evidence that listing the species as protected by law is beneficial
338 for their population growth corresponding to several other studies showing population
339 increases of legally protected species in different parts of the world (Male and Bean, 2005;
340 Voříšek et al., 2008; Koleček et al., 2014; Gamero et al., 2017). This may be a positive
341 message for conservationists involved in creation of protected species lists because it shows
342 general efficiency of this effort. However, global applicability of the findings of these studies
343 is still not inevitable for two reasons. First, all of these studies are confined to the North
344 America and Europe, i.e. the richest and the most developed regions of the world. It is well
345 known that people's awareness of environmental issues followed by development of efficient
346 solutions is often associated with obtaining a given level of economy (Dinda, 2004), as

347 depicts the Kuznets curve which has been shown applicable also for bird populations (Lantz
348 and Martínez-Espiñeira, 2008). Therefore, it is possible that the conditions in the North
349 America and Europe are simply more suitable for a higher efficiency of conservation
350 legislation in terms of scientific basis and enforcement than elsewhere. Second, the reports of
351 positive effects of legal protection on bird populations may be easier to publish in relevant
352 journals than the findings of insignificant or even negative effects, which may produce a
353 publication bias (Fanelli, 2012). Therefore, the overview based on the existing studies may be
354 perhaps too optimistic and further assessments, especially from regions other than the North
355 America and Europe, are needed to make general conclusions about the positive effects of
356 being listed as protected.

357 Our analysis controlled for the influence of a comprehensive set of traits recently being
358 recognized as important correlates of bird population trends (Reif, 2013). We found that
359 following four of these traits were significantly related to the trends together with the effect of
360 listing under the Annex I: habitat specialization, position along the habitat humidity gradient,
361 life history strategy and nest location. These results confirmed the previous findings of
362 continent-wide decline of habitat specialists leading to homogenization of bird communities
363 (Le Viol et al., 2012), which is probably caused by higher sensitivity of more specialized
364 species to various human-induced environmental impacts which recently magnify (Devictor et
365 al. 2008), whereas habitat generalists are more resilient and they can even benefit from the
366 new opportunities provided by altered habitats (Hanzelka and Reif, 2015). In contrast, the
367 observed population increase of the species associated with wetlands was rather unexpected
368 (compare with Lehikoinen et al., 2016), but corresponds to recent observations of population
369 increases of wetland birds in several European countries such as the Netherlands (Van
370 Turnhout et al., 2007) or the Czech Republic (Koleček et al., 2010) which may be attributable
371 to the increased conservation effort aimed to wetland habitats and population expansion of
372 many waterbird species following the climatic amelioration (Musil et al., 2011). We also did
373 not expect more negative trends in species with faster life history strategies since those should
374 be more resilient to environmental perturbations due to their high reproductive potential
375 (Owens and Bennett, 2000). However, it seems that the recent global change conditions may
376 indeed favour the species with slower life history strategies due to their ability to wait for
377 longer time until the conditions are more suitable for reproduction, whereas the species with
378 faster strategies (associated with shorter life span) are forced to reproduce under suboptimal
379 conditions (Sol et al., 2012) leading to their population decline. Similar results were recently
380 found in studies focusing on population of French (Jiguet et al., 2007) and Eastern European

381 birds (Koleček et al., 2014). Finally, we found some evidence that species breeding closer to
382 ground decline, supporting the findings of several other studies on European birds (Gregory et
383 al., 2007; Van Turnhout et al., 2010; Koleček et al., 2014). This pattern may mirror
384 continuation of the negative impacts of human land use in open habitats (e.g. agricultural
385 intensification) where the majority of such species breed (Butler et al., 2010), but may be also
386 attributable to the increased predation pressure from the side of recently introduced predators
387 (Chalfoun et al., 2002).

388 In conclusion, our study showed a positive influence of listing the species under the
389 Annex I of the Birds Directive on their populations in the EU member states in contrast to the
390 non-members. As birds are often taken as indicators for other groups of organisms with less
391 complete data on their population abundance (Westgate et al. 2017), we can speculate whether
392 or not the conservation benefits delivered by the EU's conservation legislation may apply also
393 to the other ecosystem components. Despite some indications that this might be the case for
394 specific groups of organisms in several countries (e.g. Cantarello and Newton, 2008; Lison et
395 al., 2013, 2015), some other studies report the opposite results (Diserens et al., 2017).
396 Therefore, a need for a continent-wide assessment similar to the one presented in this study
397 for birds, should be one of the priorities of conservation science (see also Hermoso et al.,
398 2017).

399

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404

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596

597 **Table 1:** Characterization (a) and predicted relationships to population trends (b) of the traits considered for the analysis of European bird
 598 population trends.

599

600 a)

trait ID	trait name	description
1	habitat niche position	mean of species' positions along the gradient from closed forest (1) to open treeless habitat (7)
2	habitat niche breadth	range of species' positions along the gradient from closed forest (1) to open treeless habitat (7)
3	position along the humidity gradient	species' positions along the gradient from non-humid (1) to water habitat (3)
4	relation to built-up areas	discrimination among species breeding (1) and not breeding (0) in built-up areas
5	mean latitude of breeding range	latitude of the centre of species' breeding range in Europe (in decimal degrees)
6	potential range shift	magnitude of the shift of the range centre between the current and the predicted future breeding range in Europe (in km)
7	diet niche breadth	(1) obligatory herbivorous or insectivorous/carnivorous, (2) herbivorous and insectivorous/carnivorous, (3) omnivorous
8	migratory strategy	(1) residents, (2) short-distance and (3) long-distance migrants
9	marginality of European distribution	distance between the centre of the species' European and Euroasian breeding range (in decimal degrees)
10	life history strategy	position along the slow-fast life history gradient revealed by a principal component analysis on six species' life-history traits
11	nest location	species breeding on or near ground (0), in shrubs and small trees (1), in high trees (2)

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614 b)

trait ID	predicted relationship	mechanism	reference	
1	more negative trends in species more associated with open habitats	agricultural intensification, forest encroachment on open habitats	Butler et al. 2010	615 616
2	more negative trends in more specialized species	higher sensitivity of habitat specialists to environmental change	Le Viol et al. 2012	617 618
3	more negative trends in species more associated with more humid habitats	destruction of wetlands, eutrophication, decrease in ground water level	Lehikoinen et al. 2016	616 619
4	more positive trends in species more associated with built-up areas	exploitation of free ecological space after urbanization	Evans et al. 2011	620
5	more negative trends in species breeding at higher latitudes	detrimental impact of climate change on cold-adapted species	Stephens et al. 2016	621
6	more negative trends in species with lower temperature resilience	detrimental impact of climate change on climatic specialists	Jiguet et al. 2006	622
7	more negative trends in diet specialists	higher sensitivity of diet specialists to environmental change	Van Turnhout et al. 2010	623 624
8	more negative trends in species with longer migration distance	environmental changes on wintering grounds, climate change, higher sensitivity of migrants	Finch et al. 2017	625
9	more negative trends in species with populations further from range centre	less efficient buffer to environmental perturbations in marginal populations	Diaz et al. 2015	626 627
10	more negative trends in species with slower life history strategies	lower resilience of species with low pace of life to environmental perturbations	Owens and Bennett 2008	628
11	more negative trends in species with nests located closer to ground	higher exposure of ground nesting species to the increased nest predation risk	Chalfoun et al. 2002	629 630
				631

632 **Table 2:** Characteristics of the best performing linear mixed-effects models relating
633 population trends to species' traits of European birds. Model performance was assessed by
634 Akaike information criterion (AIC_c) across the all possible combinations of the trait variables
635 and the best performing models are those with $\Delta AIC_c < 2$. See Table 1a for variable
636 identification.

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model terms	no of parametres	AIC_c	ΔAIC_c	model weight
10+11	6	5440.00	0.00	0.43
3+10+11	7	5441.59	0.59	0.32
2+3+10+11	8	5441.11	0.11	0.25

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640 **Table 3:** Relationships between population trends of European birds and listing the species
641 under the Annex I of the Birds Directive in old European union's member states (i.e. those
642 entered EU before 2004), new European union's member states (entered EU from 2004
643 onwards) and non-member states, respectively, estimated by the final linear mixed-effects
644 model taking into account the effects of the species' traits previously selected as important by
645 the information theoretic approach (see Table 2). Significant results are in bold.

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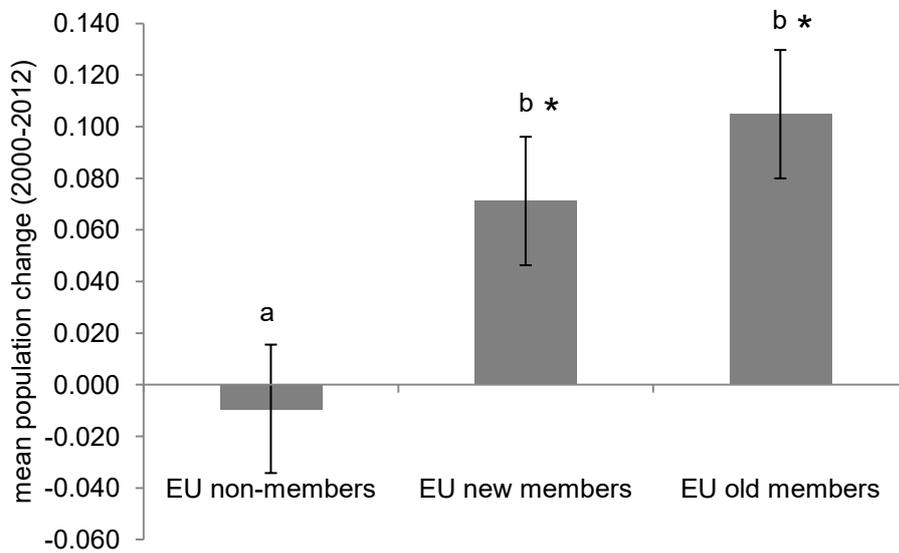
model term	coefficient	SE	df	t	P
habitat niche breadth	0.015	0.004	4420	3.32	0.001
position along a humidity gradient	0.043	0.011	4420	4.02	<0.001
life history strategy	-0.016	0.004	4420	-3.50	0.001
nest location	0.050	0.009	4420	5.67	<0.001
EU non-member states	-0.188	0.041	30	-4.63	<0.001
EU new member states	-0.180	0.039	30	-4.57	<0.001
EU old member states	-0.195	0.037	30	-5.21	<0.001
annex I in EU non-member states	-0.009	0.028	4420	-0.33	0.741
annex I in EU new member states	0.071	0.028	4420	2.53	0.012
annex I in EU old member states	0.105	0.025	4420	4.21	<0.001

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650 **Fig. 1:** Relationships between population trends of European birds and listing the species
651 under the Annex I of the Birds Directive in old European union's member states (i.e. those
652 entered EU before 2004), new European union's member states (entered EU from 2004
653 onwards) and non-member states, respectively, estimated by the final linear mixed-effects
654 model. The effects of the species' traits potentially affecting bird population trends were
655 controlled for (Table 3). The respective bars depict the effect of listing under the Annex I
656 estimated by the model for respective groups with \pm standard error. Different letters above
657 bars indicate statistically significant differences between respective groups. Astrisk above
658 bars indicates statistically significant differences from zero.
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662 **Supplementary Table S.1:** Characteristics of 252 species of European breeding birds used for the analyses. See Table 1 for the names and
663 characteristics of particular trait variables (numbered from 1 to 11). Annex I depicts listing of the species under the Annex I of the Birds
664 Directive.

Species	Annex I	1	2	3	4	5	6	7	8	9	10	11
<i>Accipiter gentilis</i>	0	2.3	3	1	0	53.18	385	1	1	64.54	-2.83	3
<i>Accipiter nisus</i>	0	2.7	3	1	0	51.37	373	1	2	55.58	-1.70	3
<i>Acrocephalus dumetorum</i>	0	3.3	3	3	0	58.09	809	1	3	24.96	1.45	2
<i>Acrocephalus paludicola</i>	1	7.0	0	3	0	51.87	489	1	3	0.00	1.41	2
<i>Acrocephalus scirpaceus</i>	0	7.0	0	3	0	48.85	401	2	3	18.39	1.62	2
<i>Acrocephalus schoenobaenus</i>	0	6.5	1	3	0	54.69	282	2	3	18.89	1.70	1
<i>Actitis hypoleucos</i>	0	6.5	1	3	0	53.90	260	1	3	63.80	-0.48	1
<i>Aegithalos caudatus</i>	0	3.0	2	1	0	49.72	466	1	1	56.98	2.09	2
<i>Aegolius funereus</i>	1	3.5	5	1	0	58.20	494	1	1	64.19	-1.12	3
<i>Alauda arvensis</i>	0	7.0	0	1	0	57.80	382	2	2	63.80	1.83	1
<i>Alcedo atthis</i>	1	7.0	0	3	0	47.57	278	1	2	53.12	1.04	1
<i>Alectoris graeca</i>	1	4.5	5	1	0	41.60	548	1	1	0.00	-1.35	1
<i>Alectoris rufa</i>	0	7.0	0	1	0	43.92	693	1	1	0.00	-0.69	1
<i>Anas acuta</i>	0	7.0	0	3	0	60.85	459	2	2	63.14	-1.66	1
<i>Anas clypeata</i>	0	7.0	0	3	0	53.96	766	2	2	57.20	-1.58	1
<i>Anas crecca</i>	0	7.0	0	3	0	56.08	587	2	2	63.61	-1.19	1
<i>Anas penelope</i>	0	7.0	0	3	0	62.91	275	1	2	63.61	-1.66	1
<i>Anas platyrhynchos</i>	0	7.0	0	3	0	52.04	269	2	2	58.34	-1.86	1
<i>Anas querquedula</i>	0	7.0	0	3	0	52.24	484	2	3	56.58	-1.21	1
<i>Anas strepera</i>	0	7.0	0	3	0	51.03	694	1	2	56.05	-1.80	1
<i>Anser anser</i>	0	5.0	5	3	0	53.68	491	1	2	45.51	-3.00	1
<i>Anthus campestris</i>	1	7.0	0	1	0	45.45	419	1	3	26.25	1.42	1
<i>Anthus pratensis</i>	0	7.0	0	2	0	56.11	575	2	2	11.76	2.02	1
<i>Anthus spinoletta</i>	0	7.0	0	1	0	44.94	757	2	2	68.47	1.71	1

<i>Anthus trivialis</i>	0	4.5	3	1	0	53.44	301	1	3	41.66	1.89	1
<i>Apus apus</i>	0	6.0	0	1	1	50.71	120	1	3	37.26	-0.01	3
<i>Tachymarptis melba</i>	0	6.0	0	1	1	41.05	421	1	3	19.26	-0.45	3
<i>Aquila adalberti</i>	1	4.0	4	1	0	38.92	414	1	1	0.00	-3.77	3
<i>Aquila heliaca</i>	1	4.0	4	1	0	45.53	857	1	2	36.10	-3.79	3
<i>Aquila pomarina</i>	1	1.5	1	1	0	51.08	719	1	3	2.53	-3.31	3
<i>Ardea cinerea</i>	0	4.5	3	3	0	50.68	458	1	2	46.82	-2.68	3
<i>Ardea purpurea</i>	1	7.0	0	3	0	46.08	457	1	3	45.15	-2.10	1
<i>Ardeola ralloides</i>	1	6.5	1	3	0	44.86	547	1	3	10.35	-1.14	2
<i>Asio flammeus</i>	1	6.5	1	2	0	57.74	610	1	2	59.88	-1.09	3
<i>Athene noctua</i>	0	5.0	2	1	1	46.51	298	1	1	42.96	-1.13	3
<i>Aythya ferina</i>	0	7.0	0	3	0	51.93	669	2	2	36.37	-1.97	1
<i>Aythya fuligula</i>	0	7.0	0	3	0	57.04	455	2	2	58.25	-1.84	1
<i>Bombycilla garrulus</i>	0	1.0	0	1	0	65.64	122	2	2	56.84	0.59	3
<i>Bonasa bonasia</i>	1	1.5	1	1	0	56.75	473	2	1	57.72	-1.19	1
<i>Botaurus stellaris</i>	1	7.0	0	3	0	50.97	747	1	2	47.26	-1.96	1
<i>Bubo bubo</i>	1	2.0	2	1	0	51.57	489	1	1	53.50	-3.21	1
<i>Bubulcus ibis</i>	0	6.0	0	3	0	38.29	367	1	1	45.95	-1.53	3
<i>Bucephala clangula</i>	0	6.0	0	3	0	59.69	469	1	2	59.13	-2.03	3
<i>Buteo buteo</i>	0	4.0	4	1	0	49.76	364	1	2	25.47	-2.70	3
<i>Buteo lagopus</i>	0	4.5	5	1	0	65.38	90	1	2	60.06	-2.44	3
<i>Buteo rufinus</i>	1	7.0	0	1	0	40.41	109	1	2	19.58	-2.77	3
<i>Caprimulgus ruficollis</i>	0	3.0	4	1	0	39.14	384	1	3	0.00	-0.02	1
<i>Carduelis cannabina</i>	0	5.0	2	1	1	48.75	254	2	2	21.16	2.35	2
<i>Carduelis carduelis</i>	0	4.3	3	1	1	47.95	275	2	2	25.47	2.17	3
<i>Carduelis flammea</i>	0	3.7	3	1	0	60.39	184	2	1	60.13	2.58	2
<i>Carduelis flavirostris</i>	0	6.5	3	2	0	60.19	67	2	2	66.39	1.89	2
<i>Carduelis chloris</i>	0	4.3	3	1	1	50.45	110	2	2	43.02	1.84	2
<i>Carduelis spinus</i>	0	3.0	2	1	0	55.73	497	2	2	47.11	2.31	3
<i>Carpodacus erythrinus</i>	0	5.5	1	2	0	56.09	811	1	3	61.08	1.30	2

<i>Erythropygia galactotes</i>	0	3.0	2	1	0	38.18	468	2	3	43.78	1.78	2
<i>Certhia brachydactyla</i>	0	2.0	2	1	0	45.35	526	2	1	0.00	2.29	2
<i>Certhia familiaris</i>	0	2.0	2	1	0	54.43	622	2	1	49.13	2.39	2
<i>Cettia cetti</i>	0	7.0	0	2	0	41.26	420	1	1	18.98	1.47	2
<i>Ciconia ciconia</i>	1	6.0	0	2	1	48.58	588	1	3	53.10	-3.32	3
<i>Ciconia nigra</i>	1	3.5	5	2	0	50.23	674	1	3	45.52	-3.46	3
<i>Cinclus cinclus</i>	0	7.0	0	3	0	52.43	147	1	1	58.31	0.46	1
<i>Circaetus gallicus</i>	1	5.0	5	1	0	42.97	532	1	3	29.26	-3.99	3
<i>Circus aeruginosus</i>	1	7.0	0	3	0	61.74	372	1	3	29.26	-2.28	1
<i>Circus cyaneus</i>	1	4.5	5	2	0	63.78	304	1	2	60.11	-1.90	1
<i>Circus pygargus</i>	1	7.0	0	2	0	61.15	403	1	3	20.21	-1.78	1
<i>Cisticola juncidis</i>	0	7.0	0	3	0	40.19	388	1	1	55.52	2.62	1
<i>Clamator glandarius</i>	0	4.0	4	1	0	40.31	481	1	3	7.89	0.46	3
<i>Coccothraustes coccothraustes</i>	0	2.5	3	1	0	49.42	529	2	2	59.06	0.76	3
<i>Columba oenas</i>	0	1.0	0	1	0	50.92	771	1	2	18.72	0.02	3
<i>Columba palumbus</i>	0	2.5	3	1	0	51.27	136	1	2	15.03	-0.38	3
<i>Coracias garrulus</i>	1	3.0	2	1	0	46.62	404	1	3	18.72	-0.69	3
<i>Corvus corax</i>	0	2.0	2	1	0	52.28	137	3	1	60.04	-1.58	3
<i>Corvus corone</i>	0	6.0	0	1	0	51.94	17	3	1	64.77	-1.04	3
<i>Corvus frugilegus</i>	0	4.0	4	1	1	50.98	594	3	2	45.17	-0.94	3
<i>Corvus monedula</i>	0	5.0	2	1	1	50.13	276	2	2	24.87	-0.54	3
<i>Coturnix coturnix</i>	0	7.0	0	1	0	47.59	333	2	3	31.46	0.07	1
<i>Crex crex</i>	1	7.0	0	2	0	52.41	615	2	3	33.75	0.43	1
<i>Cuculus canorus</i>	0	4.0	4	1	0	51.01	80	1	3	60.04	0.80	2
<i>Cyanopica cyanus</i>	0	5.0	2	1	0	39.22	289	2	1	126.14	0.39	2
<i>Cygnus cygnus</i>	1	7.0	0	3	0	63.22	267	1	2	60.04	-4.01	1
<i>Cygnus olor</i>	0	7.0	0	3	0	50.94	814	1	2	43.24	-4.01	1
<i>Delichon urbicum</i>	0	6.0	0	1	1	50.72	90	1	3	60.04	1.87	3
<i>Dendrocopos leucotos</i>	1	1.0	0	1	0	52.82	895	2	1	56.69	0.08	3
<i>Dendrocopos major</i>	0	2.5	3	1	0	51.58	381	2	1	56.69	0.68	3

<i>Dendrocopos medius</i>	1	1.0	0	1	0	49.03	621	2	1	0.00	0.86	3
<i>Dendrocopos minor</i>	0	3.0	2	1	0	53.80	384	1	1	56.69	1.48	3
<i>Dendrocopos syriacus</i>	1	4.0	0	1	0	46.36	616	2	1	16.26	0.74	3
<i>Dryocopus martius</i>	1	1.0	0	1	0	53.75	342	1	1	58.76	-0.29	3
<i>Casmerodius albus</i>	1	6.5	1	3	0	47.84	282	1	2	77.70	-2.27	1
<i>Elanus caeruleus</i>	1	4.0	4	1	0	39.55	276	1	1	97.47	-1.47	3
<i>Emberiza caesia</i>	1	5.5	1	1	0	38.09	341	2	3	0.00	1.63	1
<i>Emberiza cia</i>	0	6.0	0	1	0	41.24	676	2	1	20.00	1.58	1
<i>Emberiza cirius</i>	0	4.0	4	1	0	43.73	346	2	1	0.00	2.03	2
<i>Emberiza citrinella</i>	0	4.7	3	1	0	52.83	356	2	1	26.68	1.86	1
<i>Emberiza hortulana</i>	1	5.0	2	1	0	50.71	381	2	3	20.88	1.66	1
<i>Emberiza melanocephala</i>	0	5.0	2	1	0	41.51	191	2	3	7.43	0.84	2
<i>Emberiza rustica</i>	0	3.5	3	2	0	63.83	342	2	3	64.30	1.29	1
<i>Emberiza schoeniclus</i>	0	6.0	0	3	0	54.37	92	2	2	64.30	1.98	1
<i>Erithacus rubecula</i>	0	2.5	3	1	0	51.74	335	2	2	18.42	2.01	1
<i>Falco cherrug</i>	0	3.0	2	1	0	44.59	617	1	2	35.64	-2.38	3
<i>Falco naumanni</i>	1	6.0	0	1	0	39.88	146	1	3	35.64	-1.35	3
<i>Falco peregrinus</i>	1	4.5	5	1	0	45.80	48	1	2	64.30	-2.42	3
<i>Falco subbuteo</i>	0	3.0	2	1	0	50.54	382	1	3	58.76	-1.70	3
<i>Falco tinnunculus</i>	0	5.0	2	1	1	50.67	84	1	2	60.43	-1.29	3
<i>Ficedula albicollis</i>	1	2.5	3	1	0	49.17	614	1	3	0.00	1.40	3
<i>Ficedula hypoleuca</i>	0	2.0	0	1	0	56.35	692	1	3	19.25	1.37	3
<i>Ficedula parva</i>	1	1.0	0	1	0	52.99	937	1	3	0.00	1.45	3
<i>Fringilla coelebs</i>	0	3.7	5	1	0	50.39	91	2	2	22.81	1.96	3
<i>Fringilla montifringilla</i>	0	2.5	1	1	0	63.02	294	2	2	60.43	1.51	3
<i>Fulica atra</i>	0	7.0	0	3	0	50.07	394	2	2	47.73	-0.93	1
<i>Galerida cristata</i>	0	7.0	0	1	0	45.99	219	2	1	39.64	1.55	1
<i>Galerida theklae</i>	1	6.0	0	1	0	39.43	268	2	1	0.00	1.50	1
<i>Gallinago gallinago</i>	0	7.0	0	2	0	56.16	599	1	2	62.28	-0.71	1
<i>Gallinago media</i>	1	4.5	5	2	0	56.12	763	1	3	19.91	-1.20	1

<i>Gallinula chloropus</i>	0	7.0	0	3	0	48.74	347	2	2	19.91	-0.07	1
<i>Garrulus glandarius</i>	0	2.5	3	1	0	50.55	162	3	1	45.66	-0.21	3
<i>Gavia arctica</i>	1	7.0	0	3	0	62.13	206	1	2	60.61	-3.22	1
<i>Glareola nordmanni</i>	0	7.0	0	1	0	47.34	387	1	3	18.51	-0.40	1
<i>Glareola pratincola</i>	1	7.0	0	1	0	41.95	253	1	3	18.51	-0.39	1
<i>Glaucidium passerinum</i>	1	1.0	0	1	0	59.68	323	1	1	51.99	-0.66	3
<i>Grus grus</i>	1	7.0	0	3	0	57.90	718	2	2	51.99	-3.56	1
<i>Haliaeetus albicilla</i>	1	6.0	0	2	0	55.53	25	1	1	60.25	-3.91	3
<i>Aquila fasciatus</i>	1	6.0	0	1	0	39.68	137	1	1	35.91	-3.48	3
<i>Hieraaetus pennatus</i>	1	2.0	0	1	0	44.12	231	1	3	36.79	-2.93	3
<i>Himantopus himantopus</i>	1	7.0	0	3	0	42.94	315	1	3	42.59	-1.32	1
<i>Hippolais icterina</i>	0	3.5	1	1	0	53.42	739	2	3	18.07	1.35	2
<i>Hippolais polyglotta</i>	0	3.5	1	2	0	42.86	606	2	3	0.00	1.57	2
<i>Hippolais olivetorum</i>	1	3.0	2	1	0	38.93	299	1	3	0.00	1.13	2
<i>Hirundo daurica</i>	0	5.0	2	1	1	50.96	102	1	3	35.64	1.48	2
<i>Hirundo rustica</i>	0	6.0	2	1	0	39.80	258	1	3	60.25	1.84	2
<i>Charadrius dubius</i>	0	7.0	0	2	0	50.39	360	1	3	35.64	-0.41	1
<i>Charadrius hiaticula</i>	0	7.0	0	3	0	48.36	547	1	3	60.25	-0.69	1
<i>Chlidonias hybrida</i>	1	7.0	0	3	0	52.10	919	1	3	41.88	-0.60	1
<i>Chlidonias leucopterus</i>	0	7.0	0	3	0	50.99	917	1	3	45.05	-0.66	1
<i>Jynx torquilla</i>	0	3.5	1	1	0	52.93	332	1	3	35.64	1.71	2
<i>Lagopus lagopus</i>	0	4.5	5	2	0	62.79	209	1	1	64.38	-1.31	1
<i>Lanius collurio</i>	1	6.0	0	1	0	50.93	319	2	3	18.51	0.75	2
<i>Lanius excubitor</i>	0	4.5	3	1	0	54.32	522	1	2	5.66	0.39	3
<i>Lanius nubicus</i>	0	3.0	2	1	0	42.25	282	2	2	18.73	1.68	3
<i>Larus minutus</i>	0	7.0	0	3	0	59.23	695	1	2	43.45	-1.23	1
<i>Larus ridibundus</i>	0	7.0	0	3	0	55.37	468	3	2	56.84	-1.65	1
<i>Limosa limosa</i>	0	7.0	0	3	0	51.43	935	1	3	59.52	-1.56	1
<i>Locustella fluviatilis</i>	0	3.5	2	2	0	51.44	708	1	3	15.57	1.18	2
<i>Locustella naevia</i>	0	6.0	0	2	0	52.78	739	1	3	25.41	2.27	2

<i>Loxia curvirostra</i>	0	1.0	0	1	0	55.19	521	2	2	49.94	1.57	3
<i>Loxia leucoptera</i>	0	1.0	0	1	0	65.69	201	1	1	52.40	0.71	3
<i>Loxia pytyopsittacus</i>	0	1.0	0	1	0	62.58	307	1	1	5.64	0.38	3
<i>Lullula arborea</i>	1	4.0	4	1	0	47.68	327	2	2	0.00	1.77	1
<i>Luscinia luscinia</i>	0	2.5	1	2	0	53.13	833	2	3	21.81	1.02	1
<i>Luscinia megarhynchos</i>	0	4.0	2	2	0	45.21	245	2	3	22.87	1.04	1
<i>Luscinia svecica</i>	1	6.0	0	3	0	57.18	412	2	2	64.53	1.88	1
<i>Lymnocyptes minimus</i>	0	7.0	0	3	0	65.51	243	2	3	55.21	0.04	1
<i>Melanitta fusca</i>	0	7.0	0	3	0	65.41	77	1	2	26.47	-2.48	1
<i>Melanocorypha calandra</i>	1	7.0	0	1	0	42.27	120	2	1	14.43	1.29	1
<i>Mergellus albellus</i>	1	4.5	5	3	0	66.01	82	1	2	62.94	-1.80	3
<i>Mergus serrator</i>	0	4.5	5	3	0	62.39	275	1	2	62.94	-2.40	1
<i>Merops apiaster</i>	0	6.0	0	1	0	43.67	393	1	3	19.70	-0.08	1
<i>Mergus merganser</i>	0	6.0	0	3	0	61.94	167	1	2	62.94	-2.59	3
<i>Miliaria calandra</i>	0	6.0	0	1	0	45.98	245	2	2	16.45	1.48	1
<i>Milvus milvus</i>	1	3.0	2	1	0	47.60	373	1	2	0.00	-2.66	3
<i>Monticola saxatilis</i>	0	6.0	0	1	0	41.91	618	2	3	33.94	0.86	3
<i>Montifringilla nivalis</i>	0	7.0	0	1	0	43.73	861	2	1	26.38	0.78	3
<i>Motacilla flava</i>	0	7.0	0	2	0	51.63	283	1	3	62.94	2.02	1
<i>Muscicapa striata</i>	0	3.0	2	1	0	51.56	161	1	3	32.88	1.22	3
<i>Neophron percnopterus</i>	1	6.0	0	1	0	40.78	393	1	3	14.87	-3.54	3
<i>Nucifraga caryocatactes</i>	0	1.0	0	1	0	53.10	867	2	1	64.17	-0.42	3
<i>Numenius arquata</i>	0	7.0	0	3	0	57.17	539	2	2	42.38	-2.38	1
<i>Numenius phaeopus</i>	0	7.0	0	3	0	63.47	290	2	3	64.17	-2.01	1
<i>Nycticorax nycticorax</i>	1	6.0	2	3	0	45.09	570	1	3	42.38	-1.69	2
<i>Oenanthe hispanica</i>	0	6.0	0	1	0	279.34	279	1	3	0.00	1.97	1
<i>Oenanthe isabellina</i>	0	6.0	0	1	0	45.23	182	1	3	33.41	1.89	1
<i>Oenanthe leucura</i>	1	6.0	0	1	0	39.70	211	2	1	0.00	1.22	1
<i>Oenanthe oenanthe</i>	0	7.0	0	1	0	51.86	168	2	3	64.17	1.86	1
<i>Oenanthe pleschanka</i>	1	7.0	0	1	0	46.42	123	1	3	36.49	1.18	1

<i>Pandion haliaetus</i>	1	6.0	0	2	0	60.25	487	1	3	62.67	-3.00	3
<i>Parus ater</i>	0	2.0	2	1	0	51.36	527	2	1	62.67	2.10	3
<i>Parus caeruleus</i>	0	3.0	2	1	0	49.87	186	2	1	2.83	2.24	3
<i>Parus cinctus</i>	0	2.0	0	1	0	66.83	10	2	1	62.67	1.35	3
<i>Parus cristatus</i>	0	1.0	0	1	0	52.32	622	2	1	2.83	1.85	3
<i>Parus lugubris</i>	0	3.0	2	1	0	42.02	407	2	1	3.27	1.49	3
<i>Parus major</i>	0	3.0	2	1	0	50.87	86	2	1	54.59	2.20	3
<i>Parus montanus</i>	0	2.0	0	1	0	55.55	472	2	1	64.17	1.62	3
<i>Parus palustris</i>	0	2.0	2	1	0	49.95	542	2	1	98.63	2.18	3
<i>Passer domesticus</i>	0	5.0	2	1	1	51.51	86	2	1	45.45	2.34	3
<i>Passer hispaniolensis</i>	0	4.0	4	1	0	40.12	138	2	2	19.96	2.13	3
<i>Perdix perdix</i>	0	7.0	0	1	0	50.02	500	1	1	19.96	-0.84	1
<i>Perisoreus infaustus</i>	0	2.0	0	1	0	65.23	200	2	1	58.11	-0.19	3
<i>Pernis apivorus</i>	1	2.0	0	1	0	51.87	406	1	3	19.96	-2.63	3
<i>Petronia petronia</i>	0	6.0	0	1	0	40.35	396	2	1	35.61	0.95	3
<i>Phasianus colchicus</i>	0	5.0	2	1	0	49.05	419	2	1	43.43	-1.61	1
<i>Philomachus pugnax</i>	1	7.0	0	3	0	61.53	453	1	3	64.17	-1.09	1
<i>Phoenicurus ochruros</i>	0	5.0	2	1	1	48.10	483	2	2	32.80	1.66	3
<i>Phoenicurus phoenicurus</i>	0	3.0	2	1	0	53.25	231	2	3	27.35	1.73	3
<i>Phylloscopus bonelli</i>	0	2.0	2	1	0	43.77	514	1	3	0.00	1.84	1
<i>Phylloscopus collybita</i>	0	3.5	3	1	0	52.07	321	2	2	59.25	2.50	1
<i>Phylloscopus sibilatrix</i>	0	2.0	0	1	0	53.40	432	1	3	19.00	1.78	1
<i>Phylloscopus trochiloides</i>	0	3.0	4	1	0	57.19	870	1	3	46.95	1.84	1
<i>Phylloscopus trochilus</i>	0	3.5	3	1	0	54.87	567	2	3	64.17	1.86	1
<i>Pica pica</i>	0	5.0	2	1	0	52.27	82	3	1	64.17	-0.35	3
<i>Picus canus</i>	1	2.5	3	1	0	51.74	695	1	1	47.39	-0.12	3
<i>Picus viridis</i>	0	2.5	3	1	0	48.50	561	1	1	4.58	-0.21	3
<i>Pinicola enucleator</i>	0	1.0	0	1	0	66.30	97	2	1	64.53	0.59	2
<i>Platalea leucorodia</i>	1	6.0	0	3	0	44.99	635	1	2	45.01	-2.24	2
<i>Plegadis falcinellus</i>	1	7.0	0	3	0	44.61	357	1	3	16.80	-1.62	2

<i>Pluvialis apricaria</i>	1	7.0	0	2	0	61.98	366	2	2	26.56	-1.79	1
<i>Podiceps auritus</i>	1	7.0	0	3	0	61.74	517	1	2	64.17	-1.49	1
<i>Podiceps cristatus</i>	0	7.0	0	3	0	51.53	400	1	2	42.20	-2.14	1
<i>Podiceps grisegena</i>	0	7.0	0	3	0	53.22	734	1	2	64.17	-1.73	1
<i>Porzana parva</i>	1	7.0	0	3	0	49.39	779	1	3	17.42	0.89	1
<i>Prunella modularis</i>	0	3.0	2	1	0	53.87	339	2	2	4.43	2.09	2
<i>Pterocles alchata</i>	1	7.0	0	1	0	40.63	126	1	1	11.84	-1.29	1
<i>Pterocles orientalis</i>	1	7.0	0	1	0	39.64	307	1	1	19.26	-1.09	1
<i>Hirundo rupestris</i>	0	6.0	0	2	0	40.31	432	1	2	35.61	1.66	3
<i>Pyrhacorax graculus</i>	0	6.0	0	1	0	45.66	446	2	1	26.91	-0.81	3
<i>Pyrhacorax pyrrhacorax</i>	1	7.0	0	1	0	41.02	614	2	1	36.75	-1.04	3
<i>Pyrrhula pyrrhula</i>	0	2.5	3	1	0	53.81	421	2	2	57.93	1.43	3
<i>Regulus ignicapilla</i>	0	1.0	0	1	0	46.64	532	1	2	0.00	2.73	3
<i>Regulus regulus</i>	0	1.0	0	1	0	53.93	424	1	1	77.31	2.72	3
<i>Saxicola rubetra</i>	0	6.5	1	1	0	53.40	412	2	3	23.22	1.33	1
<i>Saxicola torquatus</i>	0	6.0	0	1	0	45.60	323	2	2	63.21	2.32	1
<i>Scolopax rusticola</i>	0	1.5	0	2	0	53.65	621	2	2	46.77	-0.55	1
<i>Serinus serinus</i>	0	3.0	2	1	1	45.75	420	2	2	0.00	2.30	2
<i>Sitta europaea</i>	0	2.5	3	1	0	49.39	496	2	1	63.21	1.03	3
<i>Sitta neumayer</i>	0	6.0	0	1	0	40.11	458	2	1	3.88	1.13	3
<i>Streptopelia turtur</i>	0	4.0	4	1	0	47.26	263	1	3	27.44	-0.13	2
<i>Strix nebulosa</i>	1	2.0	0	1	0	64.73	303	1	1	63.21	-2.32	3
<i>Strix uralensis</i>	1	1.0	0	1	0	60.00	503	1	1	51.78	-2.31	3
<i>Sturnus unicolor</i>	0	5.0	2	1	1	39.45	328	2	1	0.00	1.11	3
<i>Sturnus vulgaris</i>	0	4.3	3	1	0	52.84	231	2	2	28.58	0.71	3
<i>Sylvia atricapilla</i>	0	3.3	3	1	0	50.33	303	2	2	18.65	1.83	2
<i>Sylvia cantillans</i>	0	4.5	3	1	0	40.35	329	2	3	0.00	2.48	2
<i>Sylvia communis</i>	0	5.5	1	1	0	50.56	147	2	3	27.08	1.85	2
<i>Sylvia curruca</i>	0	4.5	1	1	1	52.94	380	2	3	38.70	2.11	2
<i>Sylvia melanocephala</i>	0	3.5	3	1	0	39.84	279	2	1	0.00	2.15	2

<i>Sylvia rueppelli</i>	1	4.5	3	1	0	37.12	388	2	3	-17.92	1.39	2
<i>Sylvia undata</i>	1	3.5	3	1	0	41.73	507	2	2	-8.23	2.25	2
<i>Tadorna tadorna</i>	0	7.0	0	3	0	44.02	62	2	1	36.28	-2.38	1
<i>Tetrao tetrix</i>	1	4.0	4	1	0	41.88	326	2	1	43.75	-1.88	1
<i>Tetrao urogallus</i>	1	1.5	1	1	0	59.33	377	2	1	38.12	-2.41	1
<i>Tetrax tetrax</i>	1	6.0	0	1	0	59.09	452	2	2	17.42	-1.83	1
<i>Tringa glareola</i>	1	4.0	6	2	0	60.95	526	1	3	62.82	-0.71	2
<i>Tringa ochropus</i>	0	3.0	5	2	0	56.99	721	1	2	53.68	-0.82	2
<i>Tringa totanus</i>	0	7.0	0	3	0	54.89	511	1	2	45.15	-1.03	1
<i>Troglodytes troglodytes</i>	1	3.7	5	2	0	50.81	222	1	1	57.63	2.17	2
<i>Turdus iliacus</i>	0	2.0	0	1	0	59.37	538	2	2	54.56	1.49	2
<i>Turdus merula</i>	0	2.7	3	1	0	49.65	128	2	1	35.75	1.17	2
<i>Turdus philomelos</i>	0	4.0	4	1	0	54.21	237	2	2	30.74	1.51	2
<i>Turdus pilaris</i>	0	3.5	1	1	0	55.68	574	2	2	43.66	0.72	3
<i>Turdus viscivorus</i>	0	2.7	3	1	0	52.31	266	2	2	28.19	0.46	3
<i>Tyto alba</i>	0	6.5	1	1	1	46.45	396	1	1	0.00	-1.15	3
<i>Upupa epops</i>	0	4.0	4	1	0	46.07	314	1	3	45.42	0.39	2
<i>Vanellus vanellus</i>	0	7.0	0	2	0	54.09	374	1	2	57.93	-1.34	1

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667 **Supplementary Table S.2:** List of 33 European countries considered for the analysis with the
668 indication of their classification according to the membership in the European Union (EU):
669 old - member states entering EU before 2004, new - member states entering EU from 2004
670 onwards, none - non-members of EU.

Country	EU membership
Albania	none
Austria	old
Belarus	none
Belgium	old
Bulgaria	new
Czechia	new
Denmark	old
Estonia	new
Finland	old
France	old
Georgia	none
Germany	old
Greece	old
Hungary	new
Italy	old
Latvia	new
Lithuania	new
Moldova	none
Netherlands	old
Norway	none
Poland	new
Portugal	old
Ireland	old
Romania	new
Russia	none
Serbia	none
Slovakia	new
Slovenia	new
Spain	old
Sweden	old
Switzerland	none
Ukraine	none
UK	old

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673 **Supplementary Table S.3:** Correlations among the trait variables used for the analysis
 674 expressed using the Pearson correlation coefficient.

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ID	Trait variable	1	2	3	4	5	6	7	8	9	10
1	habitat niche position	1.00									
2	habitat niche breadth	-0.38	1.00								
3	position along the humidity gradient	0.57	-0.27	1.00							
4	relation to built-up areas	0.05	0.05	-0.17	1.00						
5	mean latitude of breeding range	-0.02	-0.07	0.09	-0.06	1.00					
6	potential range shift	-0.05	-0.11	0.19	-0.15	-0.04	1.00				
7	diet niche breadth	-0.11	-0.02	-0.21	0.06	-0.05	-0.13	1.00			
8	migratory strategy	0.24	-0.03	0.22	0.02	0.07	0.14	-0.26	1.00		
9	marginality of European distribution	0.06	-0.02	0.27	-0.06	0.11	-0.09	0.00	-0.16	1.00	
10	life history strategy	-0.24	0.05	-0.38	0.09	0.00	-0.09	0.37	0.02	-0.21	1.00
11	nest location	-0.54	0.22	-0.47	0.23	-0.10	-0.08	0.00	-0.24	-0.02	0.01

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Manuscript III

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A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland.

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4 **A non-native woody plant compromises conservation benefits of mid-**
5 **field woodlots for birds in farmland**
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62 **Abstract**
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65 Agricultural intensification seriously threatens European farmland biodiversity. To mitigate this
66 threat, farmland habitat suitability should be improved. Mid-field woodlots surrounded by
67 intensively cultivated fields or grasslands, represent one of the promising tools for such
68 improvement. However, woodlots can be dominated by non-native plants and their impacts on
69 woodlots' function as refuges for farmland biodiversity remains unclear. Therefore, we studied
70 the impact of the invasive black locust (*Robinia pseudoacacia* L.) on bird species richness in
71 woodlots in intensively cultivated Central European farmland. We surveyed 28 mid-field
72 woodlots (13 covered by native vegetation and 15 dominated by black locust) in the Czech
73 Republic, relating the species richness of all birds, habitat specialists and habitat generalists to
74 woodlot characteristics: black locust occurrence, distance to the main forest, age of the woodlot,
75 vegetation structure and arthropod biomass (expressing food supply for birds). Our results suggest
76 that the woodlots covered by the black locust had lower species richness of all birds, habitat
77 specialists and habitat generalists than the woodlots covered by native tree species. The negative
78 impact of the invasive woody plant on birds most likely acted through changes in vegetation
79 structure since such woodlots had lower coverage of the shrub layer and less continuous canopy
80 and these vegetation characteristics were negatively related to the species richness of all birds and
81 habitat generalists, respectively. Interestingly, habitat specialists showed a significant relationship
82 to the non-native woody plant occurrence even after controlling for the effect of the changes in
83 vegetation structure suggesting that some other factors linked to the invasive woody plant
84 dominance played a role here. In any case, our study shows that even though mid-field woodlots
85 host numerous bird species, the woodlots' role in the delivery of conservation benefits for birds
86 is seriously compromised if a non-native woody plant dominates their vegetation. Therefore, from
87 the perspective of bird conservation, the native woody plant species should be used for woodlots'
88 establishment.
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93 **Keywords:**
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95 agricultural landscape, biological invasions, birds, habitat specialization, farmland biodiversity,
96 mid-field woodlots
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102 **1 Introduction**
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108 In Europe, massive biodiversity loss is well documented in agricultural landscapes (Donald et al.
109 2001; BirdLife International 2004; Attwood et al. 2008). Once heterogeneous, extensively
110 cultivated farmland providing a mosaic of habitats for many different kinds of species became
111 dominated by large blocks of intensively managed arable fields and grasslands occupied by a few
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121 6 generalist taxa (Shultz et al. 2005; Devictor et al. 2008). Such a landscape is inhospitable for the
122 7 majority of farmland species which adapted to extensive farmland management (Kosicki and
123 8 Chylarecki 2012). Under these circumstances, woodlots provide important harbours for species
124 9 unable to live in the modern intensively managed homogenous farmland (Herzon and O'Hara
125 10 2007; Štrobil et al. 2019). Their intended establishment might represent a useful tool to improve
126 11 of the state of farmland biodiversity (Marr and Howley 2018).

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131 12 However, woodlots may differ in habitat quality (Orlowski and Nowak 2005) and it is thus of
132 13 utmost importance to evaluate these habitat features in respect to their importance for biodiversity.
133 14 From this perspective, it is particularly interesting that woodlots were frequently generated using
134 15 non-native woody plant species (Fortier et al. 2015). On one hand, the woodlots dominated by the
135 16 non-native woody plants might be better for local species richness than the complete absence of
136 17 such landscape features in farmland (Benton et al. 2003). On the other hand, if the non-native
137 18 woody plants form woodlots of a suboptimal habitat quality for the majority of local species, the
138 19 function of such woodlots as biodiversity refuges is questionable and their intended establishment
139 20 should be avoided. This latter possibility is suggested by various recent studies showing adverse
140 21 impacts of plant invasions on the species richness in open habitats (Skórka et al. 2010; Hajzlerová
141 22 and Reif 2014; Rogers and Chown 2014). Thereby, the ecological role of such woodlots calls for
142 23 a comprehensive assessment.

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149 24 In order to elucidate the biodiversity consequences of plant invasions in woodlots, we focused on
150 25 birds in woodlots scattered over intensively cultivated lowland farmland in the Czech Republic,
151 26 Central Europe. In this area, woodlots are scarce, albeit important habitat for farmland birds
152 27 providing breeding opportunities, food resources and migratory stopover sites (Rajmonová and
153 28 Reif 2018). However, a large part of these woodlots is dominated by invasive tree species, mainly
154 29 black locust (*Robinia pseudoacacia*). The black locust was introduced in the second half of the
155 30 18th century as exotic species and expanded its distribution after two centuries being considered
156 31 one of the most extended invasive plant in Central Europe (Vítková et al. 2017). It has generally
157 32 negative impacts on native organisms which scale across trophic levels from primary producers
158 33 to secondary consumers (Hejda et al. 2017). In the case of birds, recent studies showed that even
159 34 though the species richness remains unchanged (Hanzelka and Reif 2016), increasing abundance
160 35 of the black locust in forest stands results in changes of species composition (Kroftová and Reif
161 36 2017). Specifically, habitat specialist species are replaced by habitat generalist ones (Hanzelka
162 37 and Reif 2015). Changes in invertebrate food supply were hypothesised as a possible driver (Reif
163 38 et al. 2016a) when the occurrence of particular arthropod species in invaded and native forest
164 39 stands was largely determined by alteration of vegetation structure following the black locust
165 40 invasion (Kadlec et al. 2018).

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180 41 Although the studies cited above gained some knowledge about possible consequences of the
181 42 black locust dominance on bird populations, all these studies were conducted in large forest tracts
182 43 and thus their applicability to the farmland context and specifically to the small-sized mid-field
183 44 woodlots remains limited. To fill this knowledge gap, we surveyed breeding bird communities,
184 45 vegetation structure and arthropod food supply for birds in 28 woodlots (13 consisting of native
185 46 tree species and 15 dominated by the invasive black locust). Using these data, we test two
186 47 hypotheses. First, woodlots provide breeding habitat for birds irrespective to native/non-native
187 48 origin of the dominant tree species. Based on this first hypothesis, we can formulate two
188 49 alternative predictions: (a) bird species richness, as well as the richness of habitat specialists and
189 50 generalists do not differ between native and black locust-dominant woodlots because neither of
190 51 both habitat types differs in vegetation structure and/or invertebrate food supply. Although this
191 52 scenario is improbable, some studies from other systems of invasive species suggest its theoretical
192 53 plausibility (e.g. Kuebbing and Nuñez 2015; Simberloff 1981). An alternative prediction of this
193 54 first hypothesis is that (b) bird species richness does not differ between the native and black locust
194 55 woodlots, even though the vegetation structure and/or food supply do differ. This might be caused
195 56 by a lack of alternatives for bird breeding in the inhospitable intensively cultivated farmland
196 57 (Chamberlain and Fuller 1999). Second, black locust woodlots do not provide breeding habitats
197 58 for birds. In that case, we predict that bird species richness, and especially the richness of habitat
198 59 specialists, will be lower in black locust than in native woodlots. Such woodlots should also
199 60 provide limited food supply and should have a simplified vegetation structure.
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212 **2 Material and methods**

213 **2.1 Study area and study plots**

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215 63 Our study was carried out in the intensive agricultural landscape of Central Bohemia, Czech
216 64 Republic, Central Europe (latitude 49°53'–50°07'; longitude 14°09'–14°27'; 160–330 m a.s.l.;
217 65 annual rainfall total 500–600 mm; annual mean temperature 8–9 °C). For our study, we selected
218 66 28 woodlots < 1.5 ha (average size: 0.38 ha; range: 0.12–1.32 ha; average age: 78.57 years;
219 67 sd:12.08 years; range: 50-110 years, see Fig. 1 in Štrobil et al., 2019), 15 of them were dominated
220 68 by the invasive black locust (*R. pseudoacacia*, henceforth: “black locust woodlots”) while the
221 69 other were composed by native deciduous tree species: dominantly by oaks (*Quercus* spp.) and
222 70 European ash (*Fraxinus excelsior* L.), mixed by hornbeam (*Carpinus betulus* L.), maples (*Acer*
223 71 spp.), limes (*Tilia* spp.) and elms (*Ulmus* spp.), henceforth: “native woodlots”. All woodlots have
224 72 been completely surrounded by intensively managed blocks of arable land.
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232 **2.2 Bird data**

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239 75 Both types of woodlots (i.e. black locust and native) were surveyed in spring 2017 to gather
240 76 information about bird occurrence. Each woodlot was visited 3 times corresponding to early (late
241 77 March), middle (mid-April) and late spring (mid-June) to capture all phases of the peak breeding
242 78 season. During each visit, the observer walked slowly through the whole area of the woodlot
243 79 recording every bird species which was heard or seen in the woodlot. Bird surveys were conducted
244 80 between dawn and 11.00 during favourable weather conditions (no rain, no strong wind). The
245 81 recorded species (n = 29, see Online Resource table 1) were classified according to their habitat
246 82 specialization index (SSI) obtained from Reif et al. (2010) as generalists and specialists,
247 83 respectively. SSI was introduced by Julliard et al. (2006) as a coefficient of variation of density
248 84 of a given species across different habitats (the higher the density variation across the habitats,
249 85 the more specialized species) and Reif et al. (2010) calculated SSIs for 137 bird species breeding
250 86 in the Czech Republic using data on species' densities collected within a national common bird
251 87 monitoring scheme of country-wide coverage. For purposes of this study, we ranked all species
252 88 according to their SSI values in descending order and considered the first half of species as
253 89 specialists and the second half as generalists following Reif et al. (2016a). Birds species richness
254 90 was calculated as the total number of bird species registered in a given woodlot across all visits.
255 91 We expressed the richness separately for all birds, specialists and generalists.

264 92 **2.3 Arthropod food supply for birds**

265 93 For information about the food supply for birds, arthropods were collected in the same woodlots
266 94 where the birds were surveyed. Three different sampling methods were used to obtain information
267 95 about different arthropod taxa taken by birds: (i) pitfall trapping (5 pitfall traps consisting of two
268 96 nested plastic cups, 94 mm in diameter and 144 mm in height, containing 4% formaldehyde
269 97 solution, and spaced 5 m apart along a straight line across each woodlot), (ii) sweep-netting
270 98 (vegetation lower than 3 m along the lane of pitfall traps was swept by a net 35 cm in diameter,
271 99 area covered 25 × 5 m) and (iii) light trapping (a single light trap equipped with two 8 W UV
272 100 LED strip lights powered by 7.2Ah/12 V lead batteries, placed in the centre of each woodlot).
273 101 Arthropod sampling took place 5 times during 2016 at monthly intervals from April to September
274 102 covering the main period of arthropod activity (Štrobl et al. 2019). Through these complementary
275 103 approaches we collected information for the major taxa included in bird food supply (Lopes et al.
276 104 2016): Chilopoda, Diplopoda, Arachnida (Aranea and Opiliones), Orthoptera, Heteroptera,
277 105 Neuroptera, Coleoptera (Carabidae, Elateridae, Staphylinidae, Silphidae, Curculionioidea) and
278 106 Lepidoptera. All captured arthropods were determined to the species level. Arthropod food supply
279 107 for birds was defined as the total arthropod biomass for each woodlot (Gullan and Cranston 1994).
280 108 It was calculated using the species-specific body lengths (extracted from literature) and the
281 109 equations relating the length to body mass described by (Hóðar 1996). The total arthropod
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110 biomass (in mg) was calculated as the sum of all individuals of each arthropod species multiplied
111 by the species-specific weight.

112 **2.4 Woodlot characteristics**

113 Each woodlot was characterized by the area of woodlot and two sets of environmental variables:
114 the first set described woodlot vegetation structure and the second set land cover composition
115 surrounding the woodlot. The area of each woodlot (in ha) was computed from aerial
116 photographs using ArcGis 10.2 software (ESRI 2011). Variables describing the vegetation
117 structure (see Online Resource 2 for the summary information) were assessed by visual
118 inspection on-site following Hanzelka and Reif (2016). We estimated percentage cover of herbs
119 < 0.5 m (herb1), herbs > 0.5 m (herb2), shrubs and small trees 1–5 m (shrub), trees 5–10 m
120 height (tree1), trees > 10 m height (tree2), the canopy and clearings (proportion of the woodlot
121 area without woody plant cover). We also estimated the proportion of trees with a diameter at
122 breast height < 0.2 m (treeS), 0.2–0.5 m (treeM) and > 0.5 m (treeT), and the numbers of dead
123 and fallen trees were counted. Surrounding land cover composition was assessed in a 500 m
124 buffer around the woodlot recognizing the following land cover types using aerial photographs
125 in ArcGis 10.2: arable land, grassland, urban habitat, rock, broad-leaved forest, coniferous forest
126 and water body. For further analysis, we reduced the number of variables using a principal
127 component analysis (PCA) performed separately for each set of variables, i.e. woodlot
128 vegetation structure variables and surrounding land cover composition variables. For the
129 selection of the axes we have applied a parsimony criterion to maximize the explained variance
130 with the lower number of axis. These axes (hereafter called vPCs based on the analysis of the
131 vegetation structure variables, and sPCs based on the analysis of the surrounding land cover
132 composition variables) were taken for further analyses together with the age (extracted from
133 forest management maps downloaded from the Forest Management Institute, www.uhul.cz) and
134 area of each woodlot and the distance to the nearest continuous forest block (calculated using
135 aerial photographs in ArcGis 10.2).

136 **2.5 Statistical Analysis**

137 As the first step, we tested whether the vegetation structure differed between the two woodlot
138 types (i.e. black locust and native). For this purpose, we conducted a redundancy analysis (RDA)
139 in CANOCO 5 statistical software (ter Braak and Smilauer 2012) where the response variables
140 were those describing the vegetation structure and the explanatory variable was the type of
141 woodlot. Second, after a prior correlation analysis (see Online Resource Table 3), we tested for
142 differences in food supply (expressed as arthropod biomass) between the woodlot types
143 generalized least squares (GLS) run within the R-package nlme (Pinheiro et al. 2017) with the
144 type of woodlot and woodlot area (log-transformed) as predictors. GLS models allow us to deal

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357 145 with spatial autocorrelation by adding a correlation matrix to the model. In this case we tested
358 146 four different correlation structures (spherical, linear, exponential, and Gaussian) and also a null
360 147 correlation structure indicating the absence of spatial autocorrelation in data. Based on the Akaike
361 148 Information Criterion (AIC), we selected the correlation structure with the best fit and used that
362 149 model type for inference. In all occasions, the models without a correlation structure were more
363 150 supported than the models containing a correlation structure indicating that spatial autocorrelation
364 151 was not an issue in these data (See Online Resource Table 4). Therefore, we report all results
365 152 based on the models without a correlation structure.

369 153 To test for differences in bird species richness between black locust and native woodlots, we used
370 154 GLS in the same way as described above to deal with the spatial autocorrelation (Online Resource
371 155 Table 5). Separate models were run for all bird species, habitat specialists and habitat generalists,
372 156 respectively, and woodlot area (log-transformed) was included in all models. In addition, to gain
373 157 deeper insights into the factors driving the bird species richness variation across the woodlots, we
374 158 modelled the species richness as a function of woodlot area (log-transformed), type, age, distance
375 159 to the closest forest, arthropod biomass, vegetation structure (vPCs) and the surrounding land
376 160 cover composition of a given woodlot (sPCs). For this purpose, we also used GLS models with
377 161 the assessment of the correlation structure. After selection of the most supported correlation
378 162 structure, we composed a global model containing all the explanatory variables together and
379 163 performed variable selection via model dredging in R-package MuMIn (Bartoń 2015) based on
380 164 AIC corrected for small sample sizes (AIC_c). From all the possible combinations of variables we
381 165 selected the best subset $\Delta AIC_c < 2$ and conducted a model averaging across these models for
382 166 inference due to the lack of a clear support for a single model. All the models were conducted in
383 167 R (R Core Team 2015).

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394 169 **3 Results**

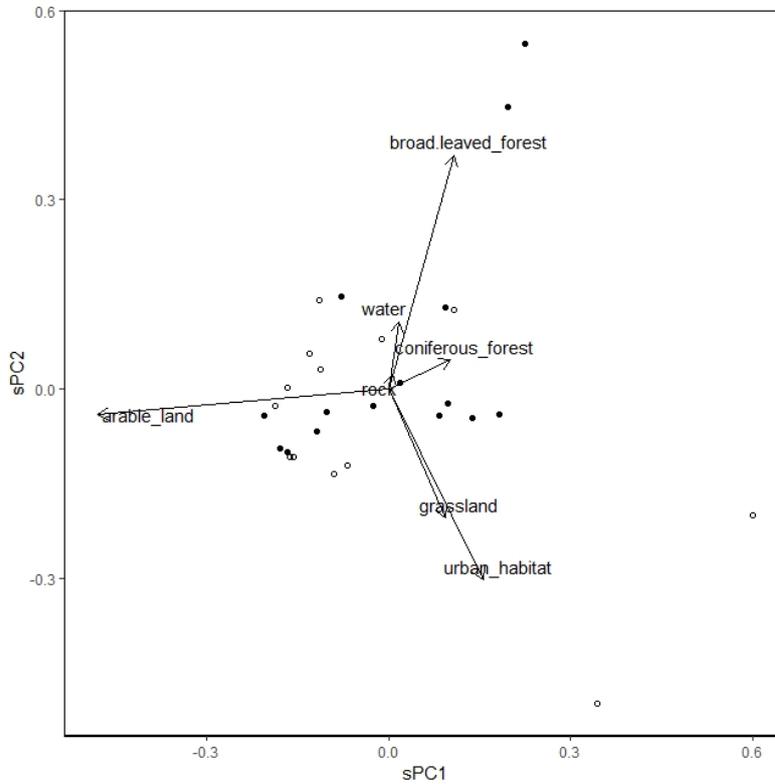
397 170 **3.1 Reduction of environmental variables using PCA**

399 171 The results of the PCA to reduce the number of variables describing surrounding land cover
400 172 composition showed that 93 % of the variance can be explained by the first two principal
401 173 components (sPC1 and sPC2, respectively). The sPC1 described a gradient discriminating
402 174 arable land from the rest of surrounding habitats, while the sPC2 showed a gradient between
403 175 broad-leaved forest versus the urban habitat and grassland (Fig. 1).

407 176 In the case of the PCA for the vegetation structure variables, the first four principal components
408 177 (vPC1, vPC2, vPC3 and vPC4) explained 83 % of the variance. The vPC1 described a gradient
409 178 from woodlots dominated by tall herbs to those with a developed shrub layer (Fig. 2). The vPC2

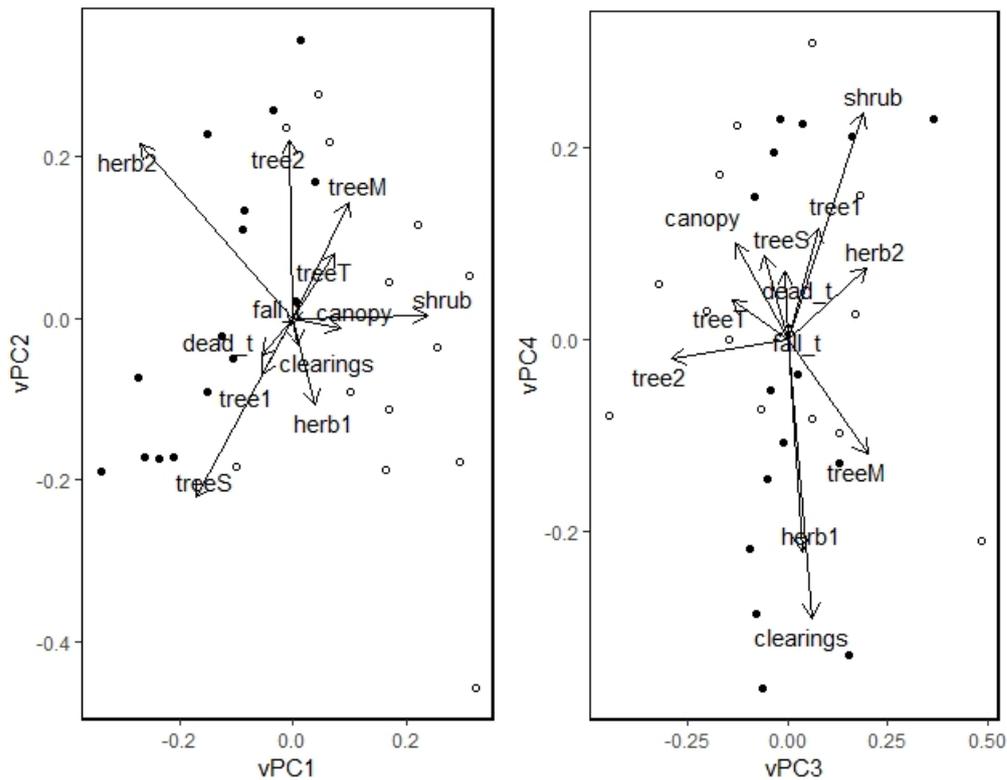
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416 179 expressed a gradient between woodlots with the thinner trunks and woodlots with tall trees (Fig.
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418 180 2). The vPC3 showed a gradient from woodlots with tall trees to woodlots with medium sized
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420 181 trunks and tall herbs (Fig. 2). The vPC4 showed a gradient from woodlots without clearings to
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422 182 woodlots with developed shrub layer (Fig. 2).



445 183
446 184 **Figure 1:** Positions of variables corresponding to particular land cover types surrounding the
447 185 woodlots along the first two axes (sPC1 and sPC2) resulting from the principal component
448 186 analysis. Native woodlots are represented by empty circles, while the black locust woodlots are
449 187 represented by bold ones.

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189 **Figure 2:** Positions of variables corresponding to particular vegetation characteristics of the
 190 woodlots along the first four axes (vPC1-vPC4) resulting from the principal component
 191 analysis. See Online Resource Table 2 for definitions of particular variables. Native woodlots
 192 are represented by empty circles, while the black locust woodlots are represented by bold ones.

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194 3.2 Habitat and food supply

195 According to the RDA, the vegetation structure significantly differed between native and black
 196 locust woodlots ($P = 0.002$; 22.6% of the explained variance). Black locust woodlots contained
 197 higher herbs, thinner trees and higher number of dead trees, while native ones had higher
 198 continuity of the canopy (Fig. 3). The bush layer was generally more prominent in native
 199 woodlots and frequently absent in black locust ones (Fig. 3). We did not find any significant
 200 difference between black locust and native woodlots with respect to total arthropods biomass
 201 (Table 1).

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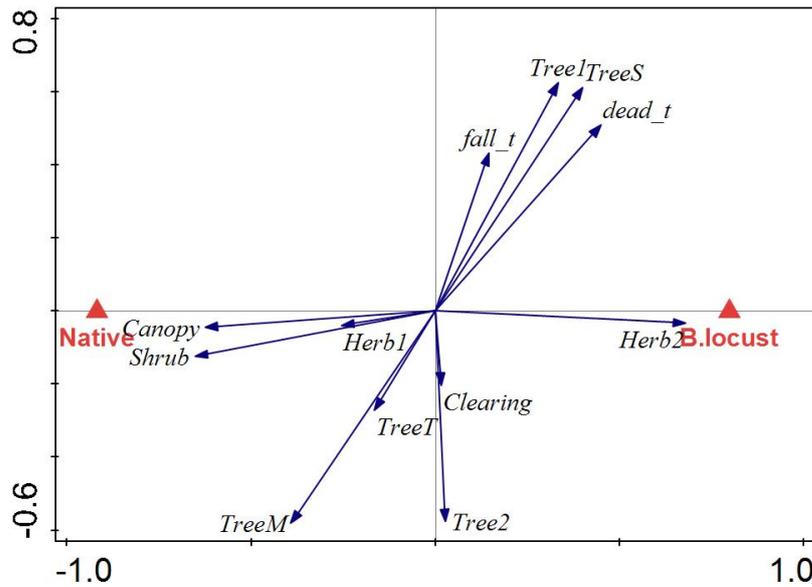


Figure 3: First two ordination axes of the redundancy analysis showing the differences in vegetation structure between the woodlots covered by native woody plant species (Native) and the woodlots dominated by black locust (B.locust). See Online Resource Table 2 for definitions of particular variables.

3.3 Bird species richness

In our surveys, we recorded 24 bird species in native woodlots and 18 species in black locust ones. The mean bird species richness per a woodlot was 6 species (\pm standard deviation = 1.73 species) in native woodlots, while 3 species (± 3.23) in black locust woodlots. The species richness of all birds, habitat specialists and habitat generalists was significantly higher in native woodlots than in black locust woodlots (Table 1).

After including all variables describing woodlot characteristics, the model dredging for the species richness of all birds showed 9 models with $\Delta AICc < 2$ (Table 2); none of them used any correlation structure. According to the results of model averaging, woodlot type, woodlot area, the vPC1, vPC3, vPC4 and the arthropod biomass were included in the best subset of explanatory variables, but the woodlot area was the only explanatory variable with a significant effect on bird species richness: it increased towards larger woodlots (Table 3).

In the case of habitat specialist bird species, the model dredging showed 2 models with $\Delta AICc < 2$ (Table 2). The model averaging of this set showed significance for the woodlot type with native woodlots being richer in more specialised species than the black locust woodlots, and for the vPC3 showing that the number of habitat specialists increases with the coverage of trees with a trunk diameter between 0.2 and 0.5 m. The best subset of explanatory variables also

225 contained the age of the woodlot, but its relationship to species richness of specialists was not
 226 significant (Table 3).

227 The analysis of species richness habitat generalist birds showed a subset of 3 models with
 228 $\Delta AICc < 2$ (Table 2). The model averaging of this subset showed a significant positive effect of
 229 the woodlot area, the vPC1 and vPC4. These PCs indicate that the bush layer seems to play an
 230 important role for habitat generalists because their richness increased towards woodlots with
 231 better developed shrub layer (Table 3). The vPC2 and the arthropod biomass were also
 232 considered in the averaged models, but no significant effects were detected (Table 3).

233 **Table 1:** Result for the generalized least square models to estimate the effects of the woodlot
 234 type (black-locust vs. native) and the woodlot area(log-transformed) on the species richness of
 235 all bird species, habitat specialist birds, habitat generalist birds and arthropod biomass,
 236 respectively.

All bird species				
	Value	Std.Error	t-value	p-value
(Intercept)	6.570	1.089	6.033	<0.001
Woodlot.Type (native)	2.874	0.866	3.320	0.002
Area	2.498	0.679	3.681	0.001
Habitat specialist birds				
	Value	Std.Error	t-value	p-value
(Intercept)	0.961	0.473	2.030	0.053
Woodlot.Type (native)	1.154	0.376	3.066	0.005
Area	0.117	0.295	0.396	0.695
Habitat generalist birds				
	Value	Std.Error	t-value	p-value
(Intercept)	5.610	0.882	6.361	<0.001
Woodlot.Type (native)	1.721	0.701	2.454	0.020
Area	2.382	0.550	4.333	<0.001
Arthropod biomass				
	Value	Std.Error	t-value	p-value
(Intercept)	41.566	12.196	3.408	0.002
Woodlot.Type (native)	13.958	9.696	1.497	0.162
Area	-1.082	7.601	-0.142	0.888

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239 **Table 2:** Characteristics of the generalized least squares models relating species richness of all bird species, habitat specialist birds and habitat generalist birds,
 240 respectively, to woodlot area (log-transformed), type (black locust and native), age, arthropod biomass, and vegetation structure (vPC1-vPC4 – see Fig2 for
 241 their meaning). The models are ranked according to the Akaike information criterion corrected for small samples (AICc) and only the top ranking models
 242 ($\Delta AICc < 2$) are shown.

All bird species						
	correlation structure	df	logLik	AICc	$\Delta AICc$	weight
Area+vPC1+vPC4	NULL	5	-57.583	127.892	0.000	0.027
Arthropods.Biomass+Area+vPC1+vPC4	NULL	6	-56.105	128.210	0.318	0.023
Woodlot.Type+Area+vPC3	NULL	5	-57.795	128.318	0.425	0.022
Area+vPC1	NULL	4	-59.462	128.664	0.771	0.019
Area+vPC1+vPC3+vPC4	NULL	6	-56.398	128.797	0.904	0.017
Arthropods.Biomass +Area+vPC1+vPC3+vPC4	NULL	7	-54.826	129.252	1.360	0.014
Woodlot.Type+Area	NULL	4	-59.851	129.442	1.549	0.013
Woodlot.Type+Area+vPC3+vPC4	NULL	6	-56.734	129.469	1.576	0.012
Area+vPC1+vPC3+vPC4	NULL	5	-58.389	129.504	1.612	0.012
Habitat specialist birds						
	correlation structure	df	logLik	AICc	$\Delta AICc$	weight
Woodlot.Type+vPC3	NULL	4	-34.182	78.103	0.000	0.049
Age+Woodlot.Type+vPC3	NULL	5	-33.550	79.826	1.723	0.021
Habitat generalist birds						
	correlation structure	df	logLik	AICc	$\Delta AICc$	weight
Area+vPC1+vPC4	NULL	5	-50.246	113.220	0.000	0.050
Arthropods.Biomass +Area+vPC1+vPC4	NULL	6	-48.863	113.726	0.505	0.039
Area+vPC1+vPC2+vPC4	NULL	6	-49.312	114.624	1.403	0.025

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Table 3: Model-averaged coefficients resulting from the top ranking generalized least square models (see Table 2) relating species richness of all birds' species, habitat specialist birds and habitat generalist birds to woodlot area (log-transformed), type (black locust and native), age and vegetation structure (vPC1-vPC4 – see Fig2 for their meaning). Variables showing significant effects are in bold.

All bird species					
	Estimate	Std.Error	AdjustedSE	z-value	Pr(> z)
Intercept	8.053	1.534	1.570	5.129	<0.001
Area	2.700	0.655	0.687	3.928	<0.001
vPC1	0.029	0.021	0.021	1.369	0.171
vPC4	0.028	0.030	0.031	0.903	0.366
Arthropods.Biomass	-0.006	0.014	0.015	0.440	0.660
Woodlot.Type (native)	0.887	1.446	1.453	0.610	0.542
vPC3	0.018	0.024	0.025	0.718	0.473
Habitat specialist birds					
	Estimate	Std.Error	AdjustedSE	z-value	Pr(> z)
Intercept	0.404	0.833	0.859	0.470	0.639
Woodlot.Type (native)	1.311	0.333	0.350	3.749	<0.001
vPC3	0.021	0.010	0.010	2.106	0.035
Age	0.004	0.010	0.011	0.418	0.676
Habitat generalist birds					
	Estimate	Std.Error	AdjustedSE	z-value	Pr(> z)
Intercept	6.820	0.926	0.961	7.098	<0.001
Area	2.431	0.482	0.507	4.790	<0.001
vPC1	0.028	0.009	0.009	3.106	0.002
vPC4	0.043	0.019	0.020	2.171	0.030
Arthropods.Biomass	-0.007	0.013	0.013	0.551	0.581
vPC2	0.004	0.010	0.010	0.383	0.701

4 Discussion

Mid-field woodlots are traditionally considered as landscape features creating heterogeneity in farmland and thus enhancing its value for biodiversity (Benton et al. 2003). However, our results provide important indication that such delivery of conservation benefits by woodlots may be seriously compromised by the dominance of an invasive woody plant supporting the prediction of our second hypothesis stating that black locust woodlots do not provide suitable habitat for birds. Specifically, woodlots covered by the invasive black locust had less developed canopy and shrub layers than the native woodlots. These differences in vegetation structure at least partly translated into the differences in bird species richness as we found that the black locust woodlots hosted lower number of bird species than the woodlots dominated by native trees. This pattern was particularly strong for habitat specialist birds. At the same time, the invertebrate food supply did not differ between black locust and native woodlots and was unrelated to bird species richness.

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263 The lower richness of bird species in black locust woodlots concerned all species, habitat generalists
264 and habitat specialists. However, once we added the woodlot vegetation structure and other ecological
265 measures into the models, the effect of the type of woodlot itself was not significant in the case of all
266 bird species and habitat generalists. It thus seems that the changes in vegetation structure caused by
267 the invasive black locust dominance were an important driver of impoverishment bird species richness
268 in invaded woodlots. Specifically, black locust woodlots had thinner trees with less continuous
269 canopy, more deadwood, less developed shrub layer and more herbs on the ground than native
270 woodlots. These vegetation characteristics are indeed those structuring communities of European
271 woodland birds (Moning and Müller 2008; Whytock et al. 2018). Moreover, habitat generalists among
272 European birds are typically those originally breeding in forest understory such as the blackcap (*Sylvia*
273 *atricapilla*), robin (*Erithacus rubecula*) or dunnock (*Prunella modularis*, Reif et al. 2016b; Tomiałojć
274 2000), and it is not surprising that the development of the shrub layer was among the key predictors of
275 species richness of habitat generalists in woodlots in our dataset.

276 Interestingly, the results differed in the case of habitat specialists for which we found the influence of
277 vegetation structure in addition to the significant effect of the black locust dominance. Therefore, it
278 seems that the changes in vegetation structure due to the black locust dominance are unable to fully
279 account for a lower number of the specialist species in invaded woodlots and some other factors
280 should play a role as well. One possibility might be that the black locust woodlots provide less food
281 resources for such specialist birds as was observed in forests (Reif et al. 2016a), but this option was
282 ruled out by the absence of difference in invertebrate food supply between the black locust and native
283 woodlots observed in our data. Therefore, we suggest that an unmeasured variable would drive the
284 pattern for habitat specialists. For instance, the delayed phenology of black locust may cause a higher
285 exposition of nests in these woodlots. In this sense, nests in black locust stands are prone to suffer
286 from high predation (Leston and Rodewald 2006; Remeš 2003) which may result in a reduction of
287 local population sizes of breeding birds and dependence of the population on immigration from other
288 sites (Pulliam and Danielson 1991). Since habitat specialists are generally rare (Gregory and Gaston
289 2000) and thus the flux of individuals from other sites cannot sufficiently compensate the losses, we
290 can speculate that the high predation pressure can mediate the effect of invasion *per se* on habitat
291 specialists persisting even after taking the vegetation structure into account.

292 Our results obtained in woodlots strikingly differ from findings of the earlier studies focused on the
293 consequences of the black locust dominance performed in continuous forest stands. In these studies,
294 habitat generalists indeed benefited from the black locust dominance in terms of their species richness,
295 while habitat specialists showed a negative impact (Hanzelka and Reif 2015). As a consequence, an
296 overall effect of the black locust on the total bird species richness was absent in forest (Reif et al.
297 2016). These differences can be explained by two important ecological drivers. First, the black locust
298 dominance had different consequences on vegetation structure in forest than in woodlots because the

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299 black locust forest stands had highly developed shrub layer (Hejda et al. 2017; Kadlec et al. 2018),
300 while the opposite was true in the case of woodlots. Since habitat generalists benefit from shrub layer
301 development (Hanzelka and Reif 2015), their species richness increased due to the black locust
302 dominance in forests in contrast to the opposite pattern in woodlots. Second, black locust-dominated
303 forest stands were surrounded by the continuous forest consisting of native trees providing suitable
304 habitat for numerous bird species (Hanzelka and Reif 2016). Therefore, even though the birds might
305 suffer to some extent from presence of the invasive woody plant in forest (Kroftová and Reif, 2017),
306 its adverse effect might be buffered by surrounding suitable habitats. Such a buffer effect cannot work
307 for the mid-field woodlots surrounded by of arable fields creating an inhospitable environment for the
308 vast majority of breeding birds. As a result, the adverse impact of the invasive woody plant can be thus
309 magnified by the isolation of woodlots (Štrobl et al. 2019).

310 For all bird species together and habitat generalists, we found out that the most important variable
311 affecting their species richness was the size of the woodlot. This result corresponds to the species-area
312 relationship and the island biogeography theory (Macarthur and Wilson 1967) when the island size
313 enhances the number of species because larger islands keep larger population sizes of the species and
314 thereby reducing their extinction probabilities (Storch et al. 2018). This is particularly the case of
315 habitat generalists originating from the forest bird species pool for which woodlots represent
316 fragments of their preferred habitat (Hofmeister et al. 2017). By contrast, any significant area effects
317 were not observed for habitat specialists. This may be explained by the frequently observed preference
318 of such species for forest edges and non-forest woody vegetation (Rajmonová and Reif 2018).
319 Availability of such habitats does not increase with woodlot size resulting in the absence of the
320 positive effect of woodlot area on the specialists' species richness (Bellamy et al. 1996).

321 Although our results show important patterns in bird species richness concerning the impact of woody
322 plant invasion on woodlot characteristics, we would like to stress one limitation of the data we have.
323 Specifically, our sampling focused on the breeding season since it is a crucial period for maintaining
324 birds' population sizes (Newton 1998), but the census technique we applied cannot prove whether the
325 observed individuals really bred in focal woodlots. It possible that some (unknown) part of species in
326 some woodlots were not breeders. However, although this fact may somewhat reduce the relevance of
327 our results in the understanding of the woodlot characteristics to support breeding bird populations, it
328 does not mean that the findings are not important for environmental management. In fact, woodlots
329 may act as steppingstones (Štrobl et al. 2019) facilitating dispersal of bird individuals through
330 unsuitable environment of intensively cultivated farmland (Rajmonová and Reif 2018). Therefore,
331 management of their habitat to maximize bird species richness is still relevant from a perspective of
332 conservation biology.

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870 333 From the applied perspective, our results support the idea of high impact of black locust on the
871 334 woodlots' vegetation structure and are thus consistent with our second hypothesis: black locust
872 335 woodlots do not offer suitable habitat for birds in the breeding season. It is likely that such negative
873 336 impacts would be the case also for other non-native woody plant species, although the studies focused
874 337 on such impacts are lacking in this landscape context (Nelson et al. 2017). Our findings are important
875 338 in the context of recent efforts to improve the value of farmland for biodiversity (Pe'er et al. 2019),
876 339 since the establishment of non-forest woody vegetation patches is one of the important tools frequently
877 340 adopted within agri-environmental schemes (Pe'er et al. 2017). When such landscape features are
878 341 created, it is essential to use solely native woody plant species for this purpose to achieve conservation
879 342 benefits for birds in farmland. Defining plausible management options for the existing black locust
880 343 woodlots is another important conservation issue.
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888 345 **5 Conclusions**

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891 346 Our results showed significant changes in the vegetation structure of the mid-field woodlots when they
892 347 are dominated by the black locust. This alteration of the vegetation structure decreases the species
893 348 richness for all birds, generalist species and specialist ones. Furthermore, specialist species are
894 349 affected by the presence of the black locust itself even after controlling for the vegetation structure,
895 350 suggesting that they are sensitive to other unidentified factor such as the phenology of the invasive
896 351 woody plant. According to our results, these woodlots are unsuitable for breeding birds and thus their
897 352 replacement by native vegetation can be recommended. However, since the other organisms may
898 353 differ in their habitat requirements from birds (cf. Štrobl et al. 2019), a broader assessment based on a
899 354 multitaxa approach is warranted before the realization of this recommendation.
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Landscape ecology

A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland

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Supplementary material

Table 1. List of all bird species recorded during our surveys, their species specialization index (SSI) extracted from Reif et al. (2010) and their classification as generalist (G) or specialist (S) for purposes of our study.

Species	SSI	Classification
<i>Anthus trivialis</i>	0.7082	G
<i>Buteo buteo</i>	0.5927	G
<i>Carduelis cannabina</i>	0.8267	S
<i>Carduelis carduelis</i>	0.6825	G
<i>Coccothraustes coccothraustes</i>	0.8013	S
<i>Columba palumbus</i>	0.4167	G
<i>Cuculus canorus</i>	0.4158	G
<i>Cyanistes caeruleus</i>	0.3869	G
<i>Dendrocopos major</i>	0.7869	S
<i>Emberiza citrinella</i>	0.6017	G
<i>Ficedula hypoleuca</i>	2.2522	S
<i>Fringilia coelebs</i>	1.3062	S
<i>Garrulus glandarius</i>	0.6083	G
<i>Lanius collurio</i>	1.2449	S
<i>Miliaria calandra</i>	1.0482	S
<i>Oriolus oriolus</i>	0.6554	G
<i>Parus major</i>	0.3701	G
<i>Passer montanus</i>	0.7504	S
<i>Phylloscopus collybita</i>	0.3367	G

<i>Phylloscopus trochilus</i>	0.7514	S
<i>Pica pica</i>	0.8316	S
<i>Picus viridis</i>	0.3581	G
<i>Serinus serinus</i>	0.8766	S
<i>Sturnus vulgaris</i>	0.7176	S
<i>Sylvia atricapilla</i>	0.3198	G
<i>Sylvia communis</i>	0.7487	S
<i>Sylvia curruca</i>	0.5762	G
<i>Turdus merula</i>	0.3409	G
<i>Turdus philomelos</i>	0.3775	G

Table 2. Abbreviations and definitions of the vegetation structure variables measured for each woodlot.

Abbreviation	Definition
Herb1	Percentage of herbs coverage >0.5 meters
Herb2	Percentage of herbs coverage <0.5 meters
Shrub	Percentage of shrub coverage (1-5 meters)
Tree1	Percentage of tree coverage (5-10 meters)
Tree2	Percentage of tree coverage (>10 meters)
Canopy	Percentage of the woodlots area covered by the canopy of tree
Clearings	Percentage of the woodlot area where the canopy is disrupted
TreeS	Proportion of trees with a diameter at breast height under 0.2 m
TreeM	Proportion of trees with a diameter at breast height between 0.2 and 0.5 m
TreeT	Proportion of trees with a diameter at breast height above 0.5 m
Dead_t	Number of dead trees within the woodlot
Fallen_t	Number of fallen trees within the woodlot

Table 3. Result of the Pearson correlation analysis for the predictors included in the models. Distance to the nearest continuous forest block, Age of the woodlot, surrounding principal components (sPC1 and sPC2) and vegetation structure principal components (vPC1-4).

	Distance	Age	Arthropods Biomass	sPC1	sPC2	vPC1	vPC2	vPC3	vPC4
Distance	1.000	0.228	0.309	-0.601	-0.068	0.333	0.015	-0.042	-0.083
Age	0.228	1.000	-0.026	-0.164	-0.254	0.199	0.274	-0.181	0.045
Arthropods Biomass	0.309	-0.026	1.000	-0.397	-0.068	0.479	0.125	0.030	0.294
sPC1	-0.601	-0.164	-0.397	1.000	<0.001	-0.264	-0.069	0.118	-0.014
sPC2	-0.068	-0.254	-0.068	0.000	1.000	-0.187	-0.094	0.220	0.200
vPC1	0.333	0.199	0.479	-0.264	-0.187	1.000	<0.001	<0.001	<0.001
vPC2	0.015	0.274	0.125	-0.069	-0.094	<0.001	1.000	<0.001	<0.001
vPC3	-0.042	-0.181	0.030	0.118	0.220	<0.001	<0.001	1.000	<0.001
vPC4	-0.083	0.045	0.294	-0.014	0.200	<0.001	<0.001	<0.001	1.000

Table 4. Performance (expressed using Akaike Information Criterion, AIC) of the generalized least squares models relating (a) species richness of all birds (Sp.Richness), (b) species richness of habitat specialist birds (Specialist.Richness), (c) species richness of habitat generalist birds (Generalist.Richness) and (d) arthropod biomass (Arthropods.Biomass) to the type of the woodlot (Woodlot.type: black locust vs. native) in respect to the correlation structure applied.

a)		
Model	Correlation structure	AIC
Sp.Richness ~Woodlot.type+Area	Null	127.702
Sp.Richness ~Woodlot.type+Area	Linear	131.702
Sp.Richness ~Woodlot.type+Area	Spherical	131.702
Sp.Richness ~Woodlot.type+Area	Gaussian	131.702
Sp.Richness ~Woodlot.type+Area	Exponential	131.702
b)		
Model	Correlation structure	AIC
Specialist.Richness ~Woodlot.type+Area	Null	81.037
Specialist.Richness ~Woodlot.type+Area	Linear	85.037
Specialist.Richness ~Woodlot.type+Area	Spherical	85.037
Specialist.Richness ~Woodlot.type+Area	Gaussian	85.037
Specialist.Richness ~Woodlot.type+Area	Exponential	85.037
c) Model		
Model	Correlation structure	AIC
Generalist.Richness ~Woodlot.type+Area	Null	115.890
Generalist.Richness ~Woodlot.type+Area	Linear	119.890
Generalist.Richness ~Woodlot.type+Area	Spherical	119.890
Generalist.Richness ~Woodlot.type+Area	Gaussian	119.890
Generalist.Richness ~Woodlot.type+Area	Exponential	119.890
d) Model		
Model	Correlation structure	AIC
Arthropods.Biomass ~Woodlot.type+Area	Null	262.990
Arthropods.Biomass ~Woodlot.type+Area	Linear	NULL
Arthropods.Biomass ~Woodlot.type+Area	Spherical	265.775
Arthropods.Biomass ~Woodlot.type+Area	Gaussian	266.990
Arthropods.Biomass ~Woodlot.type+Area	Exponential	265.983

Table 5. Characteristics of the generalized least square models relating the species richness of (a) all birds, (b) habitat specialist birds and (c) habitat generalist birds to woodlot characteristics. For each analysis (a-c) the table depicts 30 best performing models according to the Akaike Information Criterion corrected for low samples (AICc).

a) All bird species	Correlation structure	df	AICc	ΔAICc	weight
Area+vPC1+vPC4	NULL	5	127.892	0.000	0.027
Insect.Biomass+Area+vPC1+vPC4	NULL	6	128.210	0.318	0.023
Woodlot.Type+Area+vPC3	NULL	5	128.318	0.425	0.022
Area+vPC1	NULL	4	128.664	0.771	0.019
Area+vPC1+vPC3+vPC4	NULL	6	128.797	0.904	0.017
Arthropods.Biomass+Area+vPC1+vPC3+vPC4	NULL	7	129.252	1.360	0.014
Woodlot.Type+Area	NULL	4	129.442	1.549	0.013
Woodlot.Type+Area+vPC3+vPC4	NULL	6	129.469	1.576	0.012
Area+vPC1+vPC3	NULL	5	129.504	1.612	0.012
Age+Woodlot.Type+Area+vPC3	NULL	6	130.069	2.177	0.009
Area+sPC2+vPC1	NULL	5	130.097	2.204	0.009
Woodlot.Type+Area+sPC2+vPC3	NULL	6	130.170	2.278	0.009
Woodlot.Type+Area+vPC1+vPC3	NULL	6	130.279	2.387	0.008
Woodlot.Type+Area+sPC2	NULL	5	130.282	2.390	0.008
Woodlot.Type+Area+vPC1	NULL	5	130.389	2.497	0.008
Woodlot.Type+Area+vPC4	NULL	5	130.438	2.546	0.008
Woodlot.Type+Area+vPC1+vPC4	NULL	6	130.522	2.630	0.007
Area+sPC2+vPC1+vPC4	NULL	6	130.554	2.661	0.007
Woodlot.Type+Area+vPC2+vPC3	NULL	6	130.611	2.719	0.007
Age+Woodlot.Type+Area+sPC2+vPC3	NULL	7	130.739	2.847	0.007

Woodlot.Type+Area+sPC1+vPC3	NULL	6	130.748	2.856	0.007
Woodlot.Type+Area+vPC1+vPC3+vPC4	NULL	7	130.793	2.901	0.006
Arthropods.Biomass+Area+vPC1	NULL	5	130.808	2.916	0.006
Area+vPC1+vPC2+vPC4	NULL	6	130.906	3.014	0.006
Woodlot.Type+Distance+Area+vPC3	NULL	6	131.002	3.109	0.006
Woodlot.Type+Arthropods.Biomass+Area+vPC3	NULL	6	131.006	3.114	0.006
Area+sPC1+vPC1+vPC4	NULL	6	131.127	3.235	0.005
Area+vPC1+vPC4	NULL	6	131.143	3.251	0.005
Age+Area+vPC1+vPC4	NULL	6	131.164	3.271	0.005
Area+vPC1+vPC4	gaussian	6	131.165	3.273	0.005
b) Specialist birds	Correlation structure	df	AICc	ΔAICc	weight
Woodlot.Type+vPC3	NULL	4	78.103	0.000	0.049
Age+Woodlot.Type+vPC3	NULL	5	79.826	1.723	0.021
Woodlot.Type	NULL	3	80.213	2.109	0.017
Woodlot.Type+vPC2+vPC3	NULL	5	80.275	2.172	0.017
Woodlot.Type+sPC1+vPC3	NULL	5	80.446	2.342	0.015
Woodlot.Type+Arthropod.Biomass+vPC3	NULL	5	80.531	2.427	0.015
Woodlot.Type+Area+vPC3	NULL	5	80.837	2.734	0.013
Woodlot.Type+Distance+vPC3	NULL	5	81.006	2.902	0.012
Woodlot.Type+vPC3	gaussian	5	81.051	2.948	0.011
Woodlot.Type+sPC2+vPC3	NULL	5	81.062	2.959	0.011
Woodlot.Type+vPC1+vPC3	NULL	5	81.077	2.973	0.011
Woodlot.Type+vPC3+vPC4	NULL	5	81.091	2.987	0.011
Woodlot.Type+vPC3	exponential	5	81.092	2.988	0.011
Woodlot.Type+vPC3	spherical	5	81.092	2.988	0.011
Woodlot.Type+vPC3	linear	5	81.092	2.988	0.011
Woodlot.Type	linear	4	81.274	3.171	0.010
Age+Woodlot.Type+vPC2+vPC3	NULL	6	81.390	3.287	0.010
Woodlot.Type	gaussian	4	81.596	3.493	0.009
Woodlot.Type	spherical	4	81.997	3.893	0.007
Woodlot.Type+vPC2+vPC3	NULL	4	82.200	4.096	0.006
Woodlot.Type+Arthropod.Biomass+sPC1+vPC3	NULL	6	82.433	4.329	0.006
Age+Woodlot.Type+Area+vPC3	NULL	6	82.443	4.339	0.006
Woodlot.type+Arthropod.Biomass	NULL	4	82.551	4.448	0.005
Age+Woodlot.type	NULL	4	82.560	4.457	0.005
Age+Woodlot.Type+sPC1+vPC3	NULL	6	82.663	4.559	0.005
Woodlot.type	exponential	4	82.663	4.560	0.005
Woodlot.Type+sPC1	NULL	4	82.706	4.602	0.005
Woodlot.Type+sPC1+vPC2+vPC3	NULL	6	82.760	4.656	0.005
Woodlot.Type+Arthropods.Biomass+vPC2+vPC3	NULL	6	82.766	4.662	0.005
Woodlot.Type+Area	NULL	4	82.776	4.673	0.005
c) Habitat generalist birds	Correlation structure	df	AICc	ΔAICc	weight
Area+vPC1+vPC4	NULL	5	113.220	0.000	0.050
Arthropods.Biomass+Area+vPC1+vPC4	NULL	6	113.726	0.505	0.039
Area+vPC1+vPC2+vPC4	NULL	6	114.624	1.403	0.025
Area+sPC2+vPC1+vPC4	NULL	6	115.384	2.164	0.017
Area+vPC1	NULL	4	115.389	2.169	0.017
Area+vPC1+vPC3+vPC4	NULL	6	115.550	2.330	0.016
Area+sPC2+vPC1	NULL	5	115.939	2.719	0.013
Arthropods.Biomass+Area+vPC1+vPC2+vPC4	NULL	7	115.949	2.729	0.013
Arthropods.Biomass+Area+sPC2+vPC1+vPC4	NULL	7	116.283	3.063	0.011
Arthropods.Biomass+Area+vPC1+vPC3+vPC4	NULL	7	116.333	3.113	0.010
Area+sPC2+vPC1+vPC2+vPC4	NULL	7	116.388	3.168	0.010
Distance+Area+vPC1+vPC4	NULL	6	116.399	3.179	0.010
Area+sPC2+vPC1+vPC2	NULL	6	116.427	3.207	0.010
Area+sPC1+vPC1+vPC4	NULL	6	116.455	3.235	0.010
Age+Area+vPC1+vPC4	NULL	6	116.461	3.241	0.010
Woodlot.Type+Area+vPC1+vPC4	NULL	6	116.493	3.273	0.010
Area+vPC1+vPC4	exponential	6	116.493	3.273	0.010
Area+vPC1+vPC4	gaussian	6	116.493	3.273	0.010
Area+vPC1+vPC4	spherical	6	116.493	3.273	0.010

Area+vPC1+vPC4	linear	6	116.493	3.273	0.010
Area+vPC1+vPC2	NULL	5	116.608	3.388	0.009
Arthropods.Biomass+Distance+Area+vPC1+vPC4	NULL	7	116.745	3.525	0.009
Age+Arthropods.Biomass+Area+vPC1+vPC4	NULL	7	116.833	3.613	0.008
Area+vPC1+vPC2+vPC3+vPC4	NULL	7	117.179	3.959	0.007
Arthropods.Biomass+Area+sPC1+vPC1+vPC4	NULL	7	117.202	3.982	0.007
Woodlot.Type+Arthropods.Biomass+Area+vPC1+vPC4	NULL	7	117.318	4.098	0.006
Arthropods.Biomass+Area+vPC1+vPC4	gaussian	7	117.326	4.105	0.006
Arthropods.Biomass+Area+vPC1+vPC4	linear	7	117.326	4.105	0.006
Arthropods.Biomass+Area+vPC1+vPC4	exponential	7	117.326	4.105	0.006
Arthropods.Biomass+Area+vPC1+vPC4	spherical	7	117.326	4.105	0.006

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Traits and ecological space availability predict avian densities at a country
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1 Traits and ecological space availability predict avian densities at a country
2 scale

3

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15

16

17 **Abstract**

18

19 Species geographical distribution and abundances are in central focus of current ecological
20 research. Although huge amount of work has been done on their elucidation, we still miss some
21 important pieces of information. One of them is the knowledge of species' ecological traits
22 responsible for the variation in the population densities across geographical and ecological
23 space. This is crucial for understanding how ecological specialization shape species' geographical
24 distributions, a key knowledge informing about species' sensitivity to current environmental
25 challenges. Here, we precisely describe the habitat availability for individual species using high
26 resolution data collected across a whole country. In the next step, we used this information to
27 test the relationships between traits of birds and country scale estimates of population densities
28 assessed in both geographical and ecological space. The effects of the morphological and
29 reproductive traits on population densities were marginally non-significant and significant,
30 respectively, and they seem to be invariant in both geographical and ecological space. The effect
31 of the habitat specialization on population densities was negative, but it vanished once we
32 recalculated the densities for ecological space available, i.e. the area of suitable habitat. Within
33 suitable habitats, diet specialists showed relatively higher densities if compared to generalist
34 species. Our findings suggest that ecological space availability is the strongest determinant of
35 avian numbers and point at the importance of precise knowledge of species-specific habitat
36 requirements. Revival of this classical, but challenging ecological topic is needed for both proper
37 understanding of pure ecological issues and practical steps in conservation of nature.

38

39 **Keywords**

40

41 birds, abundance, ecological space, ecological traits, specialization

42

43 **Introduction**

44

45 Geographical distribution of species and individuals is in a central focus of ecology as it directly
46 influences species richness patterns (MacArthur 1984). Not surprisingly, it has attracted a lot of
47 attention up to now (Rahbek et al. 2019, Stephens et al. 2019, Mertes et al. 2020), still there are
48 significant gaps in our understanding such as fine scale information about species' distributions
49 or important pieces of knowledge on determinants of local densities and consequently
50 population sizes. Those are, however, crucial for ultimate resolution of mechanisms behind
51 spatial patterns of biodiversity as limits to number of individuals in communities as well as within
52 individual species are core parameters in biodiversity theories such as the more individual
53 hypothesis (Storch et al. 2018).

54 Local population densities are given by two types of factors. Firstly, intrinsic factors, the
55 qualities, and requirements of individual species such as body mass, territory size, life span etc.
56 In this case, body mass is a strong correlate of many other morphological, ecological, and
57 behavioural traits (Sæther 1987) and therefore frequently tested. In a short summary, higher
58 population densities are usually found in smaller species (Blackburn & Gaston 1996, Greenwood
59 et al. 1996), species with smaller propagules (Blackburn et al 1996, Böhning-Gaese & Oberrath
60 2001), species at lower position along the trophic chain (Petters & Wassenberg 1983, Arita 1993,
61 Carbone & Gittleman 2002), species with higher dispersal ability (Gaston & Kunin 1997),
62 generalist species (Brown 1984) or species specialized for an abundant resource (Gregory &
63 Gaston 2000). The last example fits also to the second group. That is extrinsic factors, which can
64 be generally considered as the availability of geographical and ecological space (e.g. estimated
65 by environmental productivity - Coe et al., 1976; Carbone & Gittleman, 2002; Pettorelli et al.,
66 2009), whose interaction is in the heart of fundamental ecological processes. From a broad
67 perspective, the role of geographical vs. ecological space in shaping community structures is
68 clearly visible under island conditions, where limited number of species allows local populations

69 reach the high numbers – density compensation hypothesis (MacArthur et al. 1972, Andrews
70 1979, Blondel 2000, Rodda & Dean-Bradley 2002, Reif et al. 2006, Buckley & Jetz 2007, Djomo
71 Nana et al. 2014). However, more effort is needed to grasp it properly on mainland due to the
72 interplay with various confounding factors.

73 It has been shown already at early stages of ecological research that population densities
74 are highest at a habitat optimum (Whittaker 1960, 1965, Brown 1984) with potentially high
75 levels of suitable resources. Moreover, co-existence with other species also affects population
76 densities in both directions, depending on how much space is for example occupied by other
77 species (Buckley & Jetz 2007). Finally, physical conditions of the environment such as
78 temperature has been tested against abundances, too (Currie & Fritz 1993). However, such a
79 relationship informs very likely about the effect of availability of resources on abundances.
80 Therefore, spatial distribution of species is strongly determined by distribution of suitable and
81 free ecological space, which suggests a link between geographical and ecological space.

82 Obviously not all geographical locations are suitable for survival and reproduction of
83 every species (Lack 1933), thus estimating densities right within ecological limits of a species
84 brings different kind of information if compared to the number of individuals per unit of
85 geographical area. Although the concept of “ecological density” (Gaston et al. 1999) is known
86 since early 20. century when reported by (Elton 1932, 1933) as “economic density”, it remains
87 seriously understudied until now. At the same time, ecological density is a very important
88 measure as it truly informs about how the species performs within *its environment*.

89 In our opinion, the concept of ecological densities is crucial for estimating ecological
90 specializations, which are currently discussed in the context of nature conservation (Devictor et
91 al. 2010, Barnagaud et al. 2011, Rivas et al. 2019) and responses of species to undergoing
92 environmental and climate changes (Julliard et al. 2004, Jiguet et al. 2007). Specialized species
93 are being revealed as endangered due to significant population decline (Gregory et al. 2004,
94 Clavel et al. 2011, Heldbjerg et al. 2018), sensitive responses to environmental changes (Purvis

95 et al. 2000; Manne & Pimm 2001, Matthews et al. 2014, Keinath et al. 2017). The sensitivity and
96 abundance of specialists, however, strongly depends on their traits as well as on availability and
97 quality of ecological space, to which they are adapted.

98 In this paper, we focused on birds as they are intensively studied, and reliable
99 information about their densities and population sizes is available. We used data about avian
100 densities collected at very local scale of few hundred meters, which properly reflects the
101 relationship of birds and their habitats. Then we analysed the data across the country scale,
102 which brings geographical distribution into play. We believe that such an approach allows us to
103 test importance of both intrinsic and extrinsic factors on observed avian densities. Specifically,
104 we asked (i) how ecological traits of birds are related to their densities, (ii) if the level of
105 ecological specialization have significant effects on avian densities and (iii) if amount of species-
106 specific ecological space reflects in species densities at the country level.

107

108 **Material and Methods**

109

110 *Birds and habitat data*

111 We used data about avian densities from the Common Bird Monitoring Program in the Czech
112 Republic (JPSP for its initials in Czech). The community structures are estimated at the census
113 points (radius 100m) located along transects, each containing 20 points, neighbouring points are
114 separated by 300-500 meters. The birds are censused during five minutes at each point and
115 every point is visited twice during the breeding season (April-June) to register the maximum
116 abundance of early and late breeding birds. We used JPSP data collected in 2009, which offered
117 best spatial coverage – information for 2580 census points along 129 transects. Prior analysis,
118 we excluded the species with low number of records (arbitrary <50 transects).

119 The JPSP data also contain the information about surrounding biotopes, in 100m radius
120 from each census point. Biotopes are classified into 12 habitat categories: coniferous forest,

121 deciduous forest, mixed forest, shrubs, meadows, field, alpine, rocks, water bodies, marshes,
122 urban and suburban. For the purpose of analyses, we have transformed those 12 habitat
123 categories into 7 categories: deciduous forest, coniferous forest, mixed forest, shrub, open
124 habitats (i.e. meadows, field, alpine and rocks), water habitats (water bodies and marshes) and
125 urban habitats (suburban and urban categories).

126

127 *Response variables*

128 Using the abundance information and the geographical area covered by the surveys we were
129 able to calculate the “geographical density” of the species. In addition, we also calculated the
130 “ecological densities”, which reflect habitat preferences of birds. Based on the species-specific
131 habitat preferences, we calculated the area of suitable habitat available for each species at each
132 point, in which it was present. We estimated habitat preferences of species at European scale.
133 The information was extracted from Storchová & Hořák (2018). In order to adjust their habitat
134 classification to our study, we merged some classes as follows: rock, savanna, tundra, grassland,
135 mountain and desserts were considered as open biotopes; reeds, swamps, fresh waters and
136 marshes were considered as water biotopes; suburban and urban environments were
137 considered as urban biotopes. The remaining habitat categories remained unchanged.

138

139 *Predictors*

140 We first run a PCA with the morphological traits – body length, wing length, tail length, bill
141 length, and *tarsometatarsus* length (data obtained from Storchová & Hořák 2018). For all
142 morphological measurements, we used means of sex-specific values. The first PC axis described
143 91% of the variance and could be interpreted as the structural size principal component (ssPC,
144 Fig. 1). Second, we run a PCA with the reproductive traits: clutch size, number of broods per year
145 egg mass and life span. The first two principal components described 79% of the variance and

146 can be understood as the slow-fast continuum principal components (sfPC, Fig. 1). Beside this,
147 we also considered the sex specific mean of the body mass as a possible predictor.

148 Further, we calculated the species specialization index (SSI, Julliard et al. 2006),
149 separately for habitat and diet specializations (SSI habitat, SSI diet) following Reif et al. (2016).
150 Habitat and dietary preferences were again extracted from Storchová & Hořák (2018). We
151 distinguish among 15 habitat categories (coniferous forest, deciduous forest, woodland, shrub,
152 savanna, tundra, grassland, reed, mountain meadows, swamp, desert, freshwater, marine, rocks
153 and human settlement) and 9 diet categories (folivore, frugivore, granivore, insectivore, other
154 invertebrates, piscivore, other vertebrates, scavenger and omnivore).

155 Finally, we used the forest dependency, the area of breeding range (henceforth range)
156 and the type of nest as additional possible predictors of the avian densities. The forest
157 dependency and the range were extracted from the BirdLife International data base (BirdLife
158 International 2004). The forest dependency distinguishes between not dependent, low-
159 dependent, medium-dependent and forest dependent species. The nest type was extracted
160 from Storchová & Hořák (2018) and classifies the nests according to their placements and
161 structures (i.e. ground, hole, open arboreal, closed arboreal, closed ground). However, due to
162 the lack of representation of species breeding on the ground and in closed arboreal nests, we
163 merged these classes with the closed ground and the open arboreal ones, respectively.

164

165 *Phylogenetic data*

166 To prevent possible phylogenetic correlation among the species of study, we extracted 1000
167 phylogenetic trees from BirdTree.org (Jetz et al, 2012). It is the largest and most complete
168 source of bird's phylogenetical data, the consensus tree was built using the R-package
169 'phytools' (Revel, 2012). The consensus tree was used to build a Brownian correlation matrix
170 using the R-package 'ape' (Paradis & Schliep, 2018) for posterior inclusion in our models.

171

172 *Statistical analysis*

173 We used phylogenetic generalized least squares models (pgls, R-package ‘nlme’, Pinheiro et al,
174 2020) to be able to include the Brownian correlation structure into our models. In our first round
175 of analyses, we related both densities, geographical and ecological, to the body mass of the
176 species using two pgls models. The variables were log-transformed in these models.
177 Furthermore, to understand how specializations affect the species density, we ran two sets of
178 pgls models, one for each log-transformed density (geographical and ecological densities). Each
179 set of models consisted into two different models relating its density to both specialization
180 indexes (SSI habitat and SSI diet) separately.

181 Secondly and to offer a full insight of how the ecological traits affect avian densities, we ran a
182 another set of pgls models for the geographical and ecological densities. Using as predictors the
183 SSI habitat, the SSI diet, the ssPC, both sfPCs (i.e. sfPC1 and sfPC2), the range, the forest
184 dependency, and the type of nest. Note that the body mass was not included in this set of
185 models due to its high correlation with the principal components of both PCAs. After
186 constructing a full model containing all the predictors mentioned above, we conducted a
187 backward stepwise variable selection. The models were simplified by withdrawing those
188 variables with higher statistical significance in every step and comparing their Akaike
189 information criterion (AIC). We stopped the variable selection once the next withdrawal
190 increased the AIC. All the analyses were conducted in R (R Core Team, 2019)

191

192 **Results**

193 The JPSP data for 2009 contained information on abundance for 47 species (after the exclusion),
194 the calculated densities ranged between 0.014 and 0.250 individual per hectare (ind/ha) for the
195 “geographical density” and between 0.046 and 6.129 ind/ha for the “ecological density”.

196

197 *Body mass – density relationships*

198 The pglS models relating the body mass of the species with both geographical and ecological
199 density did not show any significant results. Both tendencies seem to decrease the density as
200 the body mass is higher (Table 1).

201

202 *SSI – density relationships*

203 The pglS models for the geographical density versus the specialisation indexes found a significant
204 and negative effect of the SSI habitat (Table 2a, Fig. 2) but we found no significant effect of the
205 SSI diet (Table 2a). In the case of the model relating the ecological density to the specialization
206 indexes, we were not able to detect a significant effect nor tendency (Table 2b, Fig. 2) for the
207 SSI habitat, meaning that once we control for the suitable habitat available the density tends to
208 be similar among generalist and specialist species. However, the SSI diet became marginally non-
209 significant meaning that the more specialised the species diet is, the higher the density it has
210 (Table 2b).

211

212 *Effect of ecological traits on densities*

213 After the variable selection, the pglS model for the geographical density retained the SSI habitat,
214 the ssPC, sfPC1 and sfPC2 (Table 3a). The SSI habitat showed a marginally non-significant
215 negative effect over the densities. However, the ssPC showed a positive effect over the density
216 despite its statistical support was marginal. In the same way both sfPCs had a positive effect
217 over the density but this time with a high statistical significance (Table 4a). In the case of the
218 model for the ecological density, only the three principal components (ssPC, sfPC1 and sfPC2)
219 were retained after the variable selection (Table 3b), all of them with a positive effect over the
220 density. However only the sfPC were strongly significant, the ssPC only showed a marginally
221 significance (Table 4b). In other words, once we controlled for the suitable habitat available, the
222 effect of habitat specialization over the density vanished, only remaining the positive effects of
223 the principal components showing higher densities in species with larger morphological traits

224 and in those with faster life history strategies (i.e.: shorter life span, lighter eggs, higher number
225 of broods per year, lower incubation periods and bigger clutch sizes).

226

227 **Discussion**

228

229 We tested the relationships between estimates of avian population densities and morphological,
230 reproductive, and other ecological traits at a country scale of the Czech Republic. In the analysis,
231 we distinguished between population densities estimated in geographical (number of
232 individuals per unit area) and ecological space (number of individuals per unit area of suitable
233 habitat). Such a distinction has proved to be important for the strength of the observed
234 relationships. Specifically, we found that habitat specialization related negatively to the
235 population density estimated in geographical space indicating that habitat specialists have lower
236 densities than generalists. This relationship, however, disappeared when densities were
237 recalculated for ecological space available. Effect of diet specialization was much weaker
238 showing just marginally non-significant and positive effect on densities in ecological space.
239 Models with full set of predictors further corroborated influence of structural morphological and
240 reproductive traits on avian densities. However, only reproductive traits showed significant
241 positive effect on population densities in both geographical and ecological space. Specifically,
242 the PCA analysis indicated the important influence of life span and egg size. Structural size had
243 marginally non-significant effects only. We found no significant effect of body mass on avian
244 densities. Therefore, our results suggest that densities of birds are determined mostly by
245 ecological space availability and that abundances of habitat specialists and generalists do not
246 differ once their habitat requirements are considered. Moreover, we show that variation in
247 densities in ecological space is affected by diet specialization so that more specialized species
248 have higher densities. Finally, species adopting fast life-history strategies seem to achieve
249 denser populations.

250 Habitat specialists have lower densities in geographical space than habitat generalists.
251 Such a finding is not surprising given the abundance-range size relationship (Brown 1984), which
252 suggests that generalists are widely distributed and locally common. The relationship has several
253 explanations (Borregaard & Rahbek 2010) as well as exceptions (Reif et al. 2006, Ferenc et al.
254 2016) but frequently it is mechanistically attributed to larger physical area occupied by
255 generalists due to preferences for more biotope types. Therefore, given the equal distribution
256 of biotopes, generalists should have higher population densities per unit area if compared to
257 specialists. However, wider geographical distribution across more biotope types is not
258 necessarily accompanied by higher local densities (Kouki & Häyrinen 1991). Our results support
259 this, too. After controlling for suitable habitat, we observed no differences between specialists
260 and generalists in population densities. Geographical distributions of species-specific habitats
261 thus likely explain much variation in abundances observed in physical space at the country scale
262 (*cf.* Ricklefs 2013). Specialists and generalists are frequently put into contrast if contemporary
263 biotope changes (Hanh et al. 2011, Hanzelka & Reif 2015) or population declines (Gregory et al.
264 2007, Clavel et al. 2011) are tested. Generally, specialists are reported to be more sensitive to
265 environmental changes. In the light of our results, it might be caused by their restricted
266 geographical distributions as relatively higher proportions of their habitats are potentially
267 negatively affected.

268 We found a marginally non-significant positive effect of diet specialization on
269 abundances of birds within their habitats. It fits the theory that local specialization enables the
270 species to utilize the resources more effectively (Pulliam 1985), which probably makes diet
271 specialists more successful in the habitats they prefer. In birds, dietary specialization has been
272 reported to correlate negatively with estimates of abundance (Herrera 1978, De Almeida-Rocha
273 2019) and no correlation has also been reported (Brändle et al. 2002, Symonds & Johnson 2006).
274 We are not aware of any study, in which a positive correlation between abundance and diet
275 specialisation was found. This might be simply caused by considering only geographical space

276 for density estimation in these previous studies, when birds are counted also in biotopes not
277 suitable for them, which lowers estimates of population densities especially in specialized
278 species. By combining our results about habitat and diet specializations, we suggest that bird
279 densities are mostly determined by area of available habitats. As habitat selection is a strong
280 determinant of avian geographical distributions (Grinnell 1917, Telleria et al. 1992, Ricklefs
281 2013), there is presumably not enough potential for diet specializations to affect avian
282 population densities. In addition, both avian diet and abundance can be variable and respond to
283 current food supply (Korpimäki 1992, Marone et al. 2017). Such a flexibility then could confound
284 diet specialization influence on population densities.

285 The body mass is the trait most frequently tested in the context of abundance. Indeed,
286 there is a huge body of evidence about the negative relationship between body mass and
287 population densities (Cotgreave 1993, Cotgreave 1995, Blackburn & Lawton 1994), even though
288 sometimes it is reported non-significant (Blackburn & Lawton 1994, Cotgreave 1993). Still, the
289 body mass seems to be a moderate predictor of population densities (Gregory & Blackburn
290 1995). The weak relationship between body mass and avian population densities is yet not well
291 understood (Hatton et al. 2019). It might be because the strength of the body mass-density
292 relationship depends on the variance of body masses in the dataset. The large birds have surely
293 lower densities if compared to small ones since every individual need larger home range to fulfil
294 its energy requirements (Jetz et al. 2004). However, within restricted body mass variation such
295 as within taxonomical subsets or groups of similar members (such as Passerine families), we
296 might predict relatively weak body mass-population density relationship (Symonds & Johnson
297 2006) because small inter-specific differences are overridden by species idiosyncrasies in
298 ecological requirements. This may be the case of our dataset because the data come from the
299 bird monitoring programme designed to survey small territorial species being not particularly
300 suitable for larger species (Voříšek et al. 2008).

301 Body mass is correlated with many avian traits (Sæther 1987, Barbraud et al. 1999) and
302 it was true also in our data set. It was highly correlated with both morphological and
303 reproductive trait PCA axes. Thus, we decided to analyse them separately from body mass.
304 Marginally non-significant positive effects of morphology on population densities in ecological
305 as well as geographical space are hard to explain as the most influential traits seem to be wing
306 and tail lengths. Those reflect the size of the bird, which would be hypothesised to correlate
307 negatively with abundances. Likely explanation is that the contrast pattern is driven by outlying
308 species, which are structurally large and common – Magpie (*Pica pica*) and Jay (*Garrulus*
309 *glandarius*) are presumably the case species here. Their cognitive abilities (Taylor 2014) and
310 opportunistic feeding strategy (Tatner 1983, Šťastný & Hudec 2011) likely enable them to utilize
311 available resources effectively and thus live in relatively high population densities. In addition,
312 they got recently urbanized in Czechia (Šťastný & Hudec 2011) and breeding at high densities is
313 one of the characteristics of successful city dwellers (Møller 2009). As for the reproductive traits
314 we found significant effects on both estimates of population densities, for which mostly life span
315 and egg mass were responsible. It fits to the assumption that species with fast life histories live
316 in denser populations. Interestingly, the effects of other ecological traits on avian population
317 densities are not frequently tested explicitly (but see Blackburn et al. 1996, Symonds & Johnson
318 2006). The available evidence is in concordance with our results and suggests that traits
319 associated with offspring production are related to avian abundances. Besides, there is much
320 more information based on the relationship between geographic distribution and traits (Cofre
321 et al. 2007, Laube et al. 2013). Those studies observed that rarity can be linked to low
322 reproductive investment, sedentary migratory mode, low dispersal ability and habitat
323 specialization (Cofre et al. 2007, Laube et al. 2013). Although the link between abundances and
324 geographical distribution is not straightforward, it is obvious that reproductive effort, dispersal
325 ability and habitat specialization strongly determine both. More information on population
326 densities is needed in this context to provide a comprehensive picture.

327 In conclusion, our results confirmed that, apart from species specific life history, quality
328 and quantity of habitats is a crucial determinant of population densities in birds as they reflect
329 amount of suitable food resources as well as area available. Currently, human impacts on natural
330 landscapes are vastly changing distribution of indigenous biotopes and their quality, which
331 undoubtedly negatively affects bird populations. Even though the altered biotopes might
332 objectively offer high quality environments and enough food resources, the ability of birds to
333 adapt to new situations can be limited. Such a limitation potentially resides in species-specific
334 perspectives of birds on habitat requirements (Lack 1933). Those are, however, still poorly
335 known in detail as it its difficult grasp them explicitly. Thus, further research is needed to find
336 the new ways how to quantify individual ecological space requirements of birds and effectively
337 apply this knowledge in protection of avian habitats.

338

339 **Declarations**

340

341 We are grateful to Michal Ferenc, who gave advices during the pilot analysis of the data. DH
342 conceived the idea and wrote the first draft. JRS and JF analysed the data. DH, JRS and JR wrote
343 the paper.

344

345 **References**

346

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513

514 **Table 1.** Result for the pglS models relating (a) log transformed geographical density and (b) log
 515 transformed ecological density with the log transformed body mass.

516				
a)				
	Estimate	Std.Error	t-value	Pr(> t)
517				
518				
Intercept	-2.504	1.015	-2.466	0.018
Log(Body mass)	-0.189	0.142	-1.327	0.191
519				
520				
b)				
	Estimate	Std.Error	t-value	Pr(> t)
521				
522				
Intercept	-0.829	1.471	-0.564	0.576
Log(Body mass)	-0.119	0.206	-0.578	0.573
523				
524				

525 **Table 2.** Results for the pglS models relating (a) log transformed geographical density and (b) the
 526 log transformed ecological density with both SSI: Habitat and dietary

a)				
	Estimate	Std.Error	t-value	Pr(> t)
Intercept	-2.037	0.968	-2.104	0.0429
SSI habitat	-0.428	0.170	-2.525	0.0130
b)				
	Estimate	Std.Error	t-value	Pr(> t)
Intercept	-2.991	1.052	-2.843	0.0062
SSI diet	-0.047	0.249	-0.188	0.8523
a)				
	Estimate	Std.Error	t-value	Pr(> t)
Intercept	-1.600	1.468	-1.090	0.2826
SSI habitat	0.167	0.257	0.648	0.521
b)				
	Estimate	Std.Error	t-value	Pr(> t)
Intercept	-2.492	1.441	-1.730	0.091
SSI diet	0.669	0.341	1.963	0.056

537 **Table 3.** Results of the stepwise variable selection for the pglS models for: (a) Geographical
 538 density and (b) ecological density. In the tables are depicted the model formula, the variable
 539 excluded in each step (Variable) and the level of significance of the excluded variable
 540 (Significance) and its AIC score of the model.

a) Model	Variable	Significance	AIC
SSI habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2+ Range(km ²)+ Forest dependency+ Nest type	Forest dependency	0.943	-80.096
SSI Habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2+ Range(km ²)+ Nest type	Nest type	0.803	-85.158
SSI habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2+ Range(km ²)	SSI diet	0.401	-92.281
SSI habitat+ ssPC+ sfPC1+ sfPC2+ Range(km ²)	Range(km ²)	0.406	-93.441
SSI habitat+ ssPC+ sfPC1+ sfPC2	ssPC	0.070	-94.638
SSI habitat+ sfPC1+ sfPC2	-	-	-92.928
b) Model	Variable	Significance	AIC
SSI habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2+ Range(km ²)+ Forest dependency+ Nest type	Nest type	0.776	183.779
SSI habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2+ Range(km ²)+ Forest dependency	Forest dependency	0.830	176.208
SSI habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2+ Range(km ²)	Range (km ²)	0.675	172.982
SSI habitat+ SSI diet+ ssPC+ sfPC1+ sfPC2	SSI habitat	0.602	171.183
SSI diet+ ssPC+ sfPC1+ sfPC2	SSI diet	0.256	169.699
ssPC+ sfPC1+ sfPC2	ssPC	0.053	169.160
sfPC1+ sfPC2	-	-	171.294

541

542

543 **Table 4.** Detailed view of the best pglS models for (a) geographical densities and (b) ecological
 544 densities.

a)	Estimate	Std.Error	t-value	Pr(> t)
Intercept	0.124	0.084	1.478	0.147
SSI habitat	-0.029	0.015	-1.962	0.056
ssPC	0.0009	0.0004	1.857	0.070
sfPC1	0.012	0.005	2.2458	0.029
sfPC2	0.020	0.008	2.389	0.021
b)	Estimate	Std.Error	t-value	Pr(> t)
Intercept	0.367	1.253	0.293	0.771
ssPC	0.017	0.008	1.988	0.053
sfPC1	0.192	0.085	2.242	0.030
sfPC2	0.348	0.137	2.540	0.015

545

Figure 1: Details of the first two axes for both PCAs, morfological traits (left panel) and the reproductive traits (right panel).

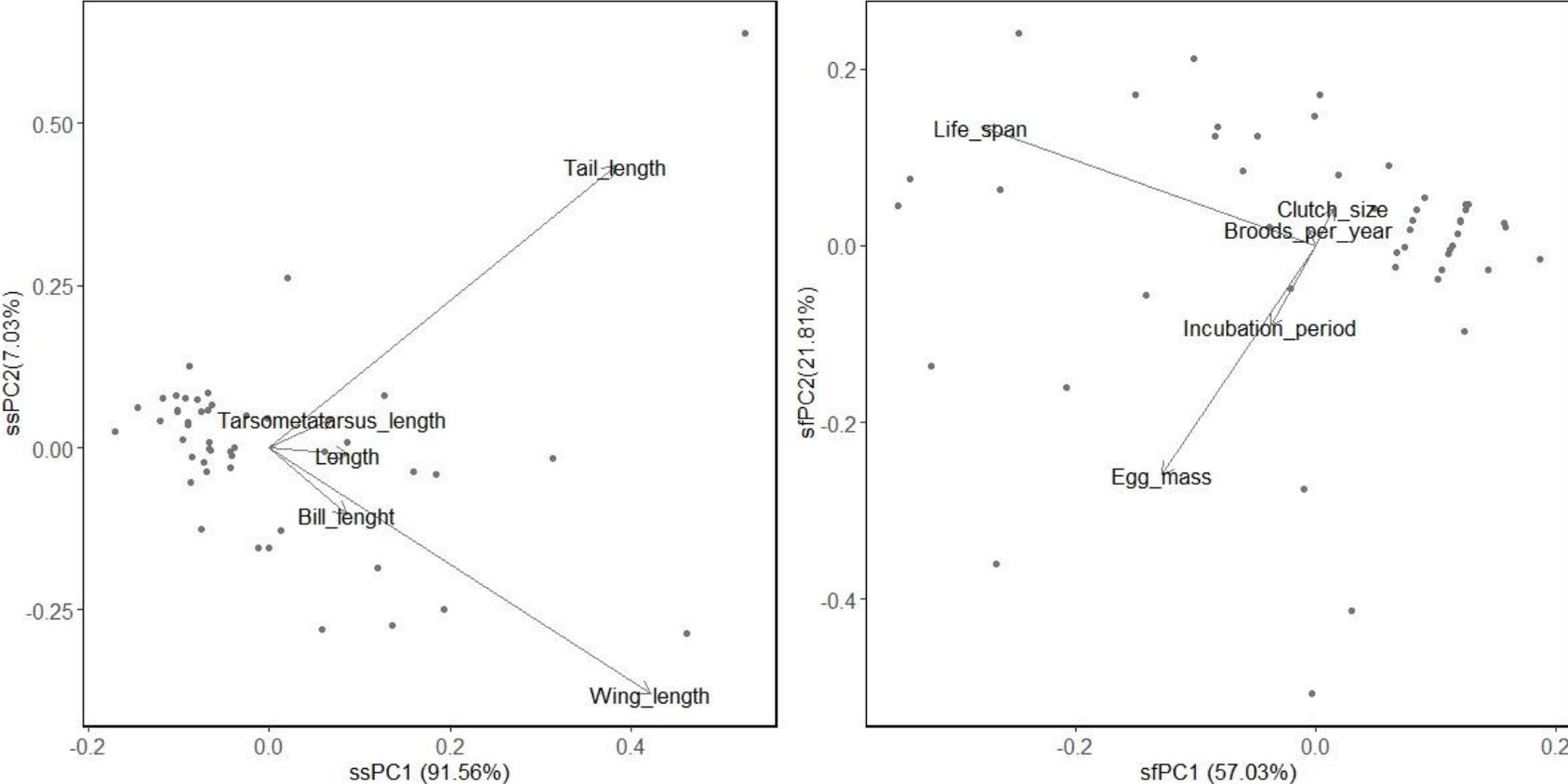


Figure 2. Relationship between the log transformed geographical densities (a) and ecological densities (b), and the habitat species specialization index (SSI.habitat), the dashed line represents the linear relationship among the variables.

