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**Changes in habitat selection patterns of the grey partridge *Perdix perdix*
in relation to agricultural landscape dynamics over the past two decades**

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Abstract

1. Changes in agricultural practices have reshaped agricultural landscapes and triggered a drastic decline in spatial and temporal heterogeneity leading to changes in habitat quality and food resources for birds. However the precise relationships between landscape changes, spatial and temporal heterogeneity, and habitat preferences in response to those changes, remain poorly known.
2. We investigated patterns of habitat selection and causes for changes over the years 1997-2017 for the grey partridge *Perdix perdix*, an iconic farmland species which has experienced a severe decline since the 1950's. Using a long-term (1997-2017) dataset collected over 435

26 km², we modeled relationships between annual land-cover maps and partridge sightings over
27 17 five-year moving windows, assessing the effects of landscape metrics, the strength of the
28 relationships, and the dynamics of habitat suitability.

29 **3.** We detected a shift in grey partridge habitat preferences over time, toward more risky
30 habitats. Avoidance of predator reservoirs (woodlands and buildings) has weakened and
31 selection of human infrastructure, such as roads and tracks, has increased. Since 1997, the
32 mean size of suitable patches has also decreased by about 26%.

33 **4.** We have interpreted these changes in habitat selection as being the result of decreasing
34 habitat quality and the increasing prevalence of captive-reared birds, currently released in
35 their thousands in the study site.

36 **5. *Synthesis and applications.*** The grey partridge has not adjusted well to changes in farming
37 practices and the low, still decreasing, population density suggests that it is not sustainable,
38 despite local initiatives and the investment in captive-bird releases. We emphasize that efforts
39 must be redirected towards habitat improvement to restore the density of refuge cover,
40 insects and seeds in the landscape, hunting management to ensure self-sustainable
41 populations and massive releases of high-quality birds. Only integrated local management,
42 involving hunters, farmers, gamekeepers and scientists can ensure the recovery of this
43 species.

44

45

46

47 **Key words**

48 Agricultural landscapes, Farmland birds, Grey partridge, Habitat quality, Habitat selection, Habitat
49 suitability maps, Long-term trends, *Perdix perdix*.

50

51 **Introduction**

52 For decades, evidence has accumulated that the main driver of the decline in farmland biodiversity
53 lies in the rapid post-war changes in agricultural practices (Benton, Vickery, & Wilson, 2003; Krebs,
54 Wilson, Bradbury, & Siriwardena, 1999; Robinson & Sutherland, 2002). Agricultural intensification
55 and specialization have reshaped and simplified agricultural landscapes (Benton et al., 2003). The
56 resulting loss of spatial and temporal heterogeneity has degraded habitat quality and food resources,
57 resulting in severe declines in European farmland birds (Benton et al., 2003; Chamberlain, Fuller,
58 Bunce, Duckworth, & Shrubbs, 2000; Robinson & Sutherland, 2002). Though agricultural landscapes
59 cover about 40% of the earth's terrestrial biomes, and are highly dynamic, long-term changes in
60 agricultural landscapes have seldom been quantified: only seven (3%) in a review of 244 studies
61 assessing land-cover changes (Uuemaa, Mander, & Marja, 2013). The scarcity in such studies comes
62 from the challenge of accessing land-cover data over the long term (Bertrand, Burel, & Baudry, 2016)
63 as well as the complexity of analyzing interacting landscape features, each with their own spatio-
64 temporal dynamics. For instance, in intensive agricultural landscapes, buildings, roads, hedgerows
65 and woodlands have broadly remained stable over the years, while crops change annually in a quasi-
66 stochastic spatial pattern of crop rotation (Bretagnolle et al., 2018b). As a result, very few studies
67 have investigated the temporal changes in habitat selection by farmland birds associated with the
68 temporal changes in the agricultural landscape (but see Brambilla et al., 2010), despite the behavioral
69 process of habitat selection being critical in determining population dynamics, survival, and
70 productivity (Jones, 2001).

71 The grey partridge *Perdix perdix* L. used to be one of the most common farmland birds in
72 Europe, but has been in a steep, widespread decline since the mid-20th century (Aebischer & Potts,
73 1994; Gée, Sarasa, & Pays, 2018; Sotherton, Aebischer, & Ewald, 2014). In many European countries,
74 numbers are at less than 10% of their pre-war level (Aebischer & Kavanagh, 1997). For example, the
75 drop in abundance was estimated at 92% between 1970 and 2015 in the UK, and it is now a red-listed

76 species in the UK Birds of Conservation Concern (Hayhow et al., 2017). Despite a decline of 23% in
77 abundance from 1989 to 2015 (Vigie-Nature, 2018) and 20% in the distribution range from 1985 to
78 2013 (Comolet-Tirman et al., 2015), grey partridge is still considered as 'Least Concern' in France. The
79 decline was attributed to three main causes, all linked to the decrease in habitat quality resulting
80 from agricultural intensification: the loss of breeding habitat, the decrease in availability of insects for
81 chicks, and the concentration of partridges and predation pressure in remaining habitats (Aebischer
82 & Ewald, 2012). Grey partridge habitat selection has been well studied: at a large scale, the species
83 avoids woodlands, associated with high predation risk, as woodlands are predator reservoirs
84 (Dudzinski, 1992), and also avoids the proximity of buildings with their predation risks from cats and
85 mustelids (Reitz, Le Goff, & Fuzeau, 2002). At a more local scale, during the breeding season, grey
86 partridges were found to be attracted by cereal cover, with a high nesting success rate, (Bro, Reitz, &
87 Mayot, 1998; Bro et al., 2013), rape and grassy covers (Birkan, Serre, Skibnienski, & Pelard, 1992; Bro
88 et al., 2013), crop diversity (Reitz et al., 2002) and linear features such as hedgerow fragments, roads
89 and tracks (Blank, Southwood, & Cross, 1967; Bro et al., 2013; Potts & Aebischer, 1991), even though
90 these linear features are associated with lower nesting success (Bro et al., 1998). However, with a
91 few exceptions (Reitz et al., 2002; Ronnenberg, Strauß, & Siebert, 2016), in most studies, the effects
92 of landscape features have been studied independently from each other so that the relative
93 contributions of different landscape features on grey partridge habitat selection remain unknown.
94 Even less is known about potential changes in patterns of habitat selection over time in highly
95 dynamic agricultural landscapes.

96 Here we investigated long-term trends in grey partridge habitat preferences in a French
97 farmland landscape, through a multi-step approach using data collected annually in an area of 435
98 km² over 21 years (from 1997 to 2017). We first identified the key landscape features that explain the
99 grey partridge occurrence over 1997-2017 studying the variable contributions to the probability of
100 occurrence. Contributions reflect the importance of variables to explain (or predict) the occurrence of

101 a species, and are commonly used to identify the key drivers of species distribution (e.g. Bellard,
102 Leroy, Thuiller, Rysman, & Courchamp, 2016; Wilson, Sexton, Jobe, & Haddad, 2013). Secondly, to
103 explore whether and how the habitat selection patterns have varied with changes in the landscape,
104 we quantified changes in the relative contributions and effect of landscape features on grey partridge
105 occurrence with time, over 17 five-year moving windows. Thirdly, we investigated whether overall
106 habitat suitability for grey partridge has changed over time, using as reference the oldest habitat
107 preferences of grey partridge available (i.e. models based on data from 1997-2001) (see Pearman,
108 Guisan, Broennimann, & Randin, 2008). In this study area, significant changes in land-cover, for
109 example a 20% increase in cereal cover since 1994 (Bretagnolle et al., 2018b), and a decrease in
110 insect availability (Bretagnolle et al., 2011) have been recorded while observed partridge densities
111 have strongly decreased (Fig. 1b) despite huge annual releases of captive-reared birds to maintain
112 local partridge populations (Bro & Crosnier, 2012). Given this observed decline in the study
113 population associated with the relatively stable amount of captive-reared grey partridges annually
114 released in France from 1995 to 2015 (around 2 million individuals in Bro, 2016), we therefore,
115 assumed that the population in our study area has changed from mainly wild birds in the nineties to
116 mainly released captive-reared birds currently. We thus suggested the massive releases of captive-
117 reared birds as a potential driver of changes in the pattern of habitat preferences. Indeed, we might
118 expect that naïve partridges would be less likely to avoid predator-rich habitats. If there has been a
119 general decline in habitat quality, partridges may select the least altered or highest quality habitats.
120 Although habitat selection is density dependent (Morris, 1989), over the same period the population
121 of partridges has strongly declined, so that habitat preferences may have remained targeted to the
122 highest quality habitats.

123

124 **Material & methods**

125 Study site and environmental layers

126 The Long-Term Socio-Ecological Research platform (LTSER) “Zone Atelier Plaine & Val de Sèvre” is
127 located in Central Western France, Nouvelle-Aquitaine region (Fig. 1a, Bretagnolle et al., 2018b). This
128 area is characterized by an intensive agricultural landscape for cereal production. Land-cover has
129 been exhaustively surveyed annually from 1994 onwards using more than 40 crop categories. Winter
130 cereals largely dominate (41.5%, mean value calculated over the years 2009 to 2016), followed by
131 sunflower (10.4%), maize (9.6%), rape (8.3%) and meadows (13.5%). Woodland fragments represent
132 2.9% of the study area (excluding the Chizé forest), and built-up areas (including isolated buildings),
133 9.8%. A preliminary analysis of landscape features showed that the density of hedgerows, buildings
134 and woodlands have varied little whereas the areas of cereals, meadows and rape, as well as crop
135 diversity and the size of crop patches have changed far more over the period (Fig. 1c-d, Fig. S1 and
136 Table S1 for statistical details). In addition, crop locations change annually because of crop rotation.

137 The vector based GIS was first transformed into a grid of 200*200 m² cells (4 ha), using R (R
138 Core Team, 2017) and QGIS (Quantum GIS Development Team, 2017), excluding all pixels that had
139 less than half their area intersecting with the study area. The pixel size was chosen to have a
140 meaningful fine scale resolution in relation to landscape dynamics that was close to the average field
141 size (Bretagnolle et al., 2018b). Landscape features already identified in the literature as being
142 selected by grey partridges were chosen for analyses as potential predictors of the grey partridge
143 occurrence: cereals, rape, meadows, hedgerows, roads and tracks (Birkan et al., 1992; Blank et al.,
144 1967; Bro et al., 2013), and woodland and buildings, features that partridges avoid (Dudzinski, 1992;
145 Reitz et al., 2002). The landscape metrics (i.e. layers assessing landscape features) used in the
146 analyses comprised the densities of various landscape features (the area in ha, or length in meters, of
147 each landscape feature divided by area of the pixel in ha), the crop diversity (Shannon-Wiener
148 diversity index calculated for five main crops (cereals, rape, meadow, maize, and sunflower), and
149 “other crops”), the mean size of the crop patches (mean area of the patches of the main crops
150 intersecting each pixel), and the distances from features avoided by partridges (distances from the

151 center of the pixel to the closest woodland and closest building) (Table S2). Each of these seven
152 metrics was calculated for each of the 21 years from 1997 to 2017 giving 147 map layers. Roads,
153 tracks, and hedgerows have remained fairly stable over the period (Appendix A, Fig. S1) so one map
154 layer was used for roads and tracks and three layers for hedgerows in 2006, 2011 and 2014 when
155 aerial photographs were available. A total of 151 layers were, therefore, included.

156

157 Partridge data

158 In total, there were 989 sightings of grey partridges in three distinct datasets covering 1997 to 2017
159 (Fig. 1e). The largest dataset (90% of total data), comprised opportunistic sightings either when
160 ornithologists working in the LTSER were studying other bird species (Bretagnolle et al., 2018b) and
161 saw partridges, or during the land-cover surveys carried out twice a year systematically over the
162 entire study site. Each year, opportunistic sightings were reported daily between late March and late
163 July (see Fig. 1f). In this dataset, the observation effort is not standardized and reporting is not
164 systematic. In the second dataset, with 5% of total sightings, observation pressure is standardized as
165 this dataset collates the results from systematic bird point counts since 1995 (see Brodier, Augiron,
166 Cornulier, & Bretagnolle, 2014 for methods). The number of point counts has increased from 160
167 (1995-2008) to about 450 since 2009, spread over the whole of the LTSER (Bretagnolle et al., 2018a).
168 Count duration was either 5 or 10 minutes (see Brodier et al., 2014) between 7:00 am to 11:00 am,
169 without call playback. The third dataset, with 5% of total sightings, collates the results of
170 standardized call playback counts specifically for both grey partridges and red-legged partridges
171 *Alectoris rufa* L., in March-April 2016 (140 sites) and 2017 (275 sites), either in the morning (from
172 7:00 am to 11:00 am) or evening (from 5:00 pm to 9:00 pm). Count duration was 10 min. In all three
173 datasets, the location of the birds, the date and time, and the number of birds were recorded. We
174 restricted our analyses to data collected during the breeding season, from late March until July (Fig.
175 1f), using the data in all three datasets.

176

177 Species distribution models

178 A multi-step approach using species distribution modeling was carried out to (1) identify key
179 landscape features and their effect on the grey partridge occurrence over the entire period 1997-
180 2017; (2) explore trends in the contribution of key features and in their effect over 17 successive 5-
181 year moving periods; (3) assess changes in habitat suitability for grey partridge over time.

182

183 Modeling process

184 The following modeling process was first applied over the entire study period (1997-2017) to
185 investigate the general pattern of habitat selection. Each landscape metric was pooled over the
186 entire study period 1997-2017 (calculating an average value by pixel). To perform the trend analysis
187 assessing changes in habitat selection patterns, the modeling process was also applied using a five-
188 year moving window, giving 17 successive 5-year periods from 1997-2001 to 2013-2017, to have
189 between 100 and 300 sightings at each time step (see Barbet-Massin, Jiguet, Albert, & Thuiller, 2012).
190 Each landscape metric was thus also pooled by 5-year periods.

191 We began by selecting uncorrelated landscape metrics to ensure the validity of the
192 predictions (Barbet-Massin & Jetz, 2014) using the method described by Leroy et al. (2013), resulting
193 in nine uncorrelated explanatory variables for the dataset with 5-year moving windows (Table S2),
194 however the rape density was excluded for modeling the dataset aggregated over the whole period
195 (Appendix B). Secondly, to select the modeling technique (Elith, Ferrier, Huettmann, & Leathwick,
196 2005), we used version 2.0 BIOMOD multi-model platform (Thuiller, Lafourcade, Engler, & Araújo,
197 2009) implemented in R. This can (1) use heterogeneous data from different counting methods
198 (Farashi & Shariati, 2017; Jackson, Gergel, & Martin, 2015) and (2) compare the most frequently used
199 modeling techniques (Barbet-Massin et al., 2012; Monnet, Hingrat, & Jiguet, 2015) (see Appendix C).
200 As these modeling techniques require presence and absence data but as our dataset did not contain

201 true absences (the absence of a sighting does not imply the absence of partridges), we generated 100
202 replicates of 1000 random pseudo-absences to obtain reliable confidence intervals (Barbet-Massin et
203 al., 2012) (Appendix C gives the methods and numbers of pseudo-absences). Generalized linear
204 models (GLM, binomial response variable, logit link) were selected for the rest of the analyses as they
205 showed a high true skill statistic ($TSS = sensitivity + specificity - 1$) (Allouche, Tsoar, & Kadmon, 2006)
206 and high sensitivity (Appendix C). For each period, the models were calibrated on a random subset of
207 70% of the presence / pseudo-absence data, and then cross-validated using the remaining 30%: this
208 cross-validation was performed three times (Thuiller, Lafourcade, & Araujo, 2009). The TSS was used
209 to evaluate the predictive performance: TSS ranges from -1 to 1, where 1 represents perfect
210 agreement while scores ≤ 0 represent a performance no better than random (Allouche et al., 2006).
211 For each period, the mean TSS was calculated averaging each model's TSS. The final calibration of
212 each model used 100% of the available data.

213

214 Assessing the contribution of each landscape metric

215 The average contribution of each landscape metric on the probability of the occurrence of grey
216 partridge was determined for the entire period 1997-2017, and for each of the successive 5-year
217 periods using the *biomod2 variables importance* function. First, a standard prediction of grey
218 partridge probability of occurrence is made across all pixels of the study area from a model calibrated
219 with all explanatory variables. Then, the values of a given variable are randomly permuted across
220 pixels and a new prediction is made. The contribution of the given variable to the prediction of the
221 probability of occurrence is 1 less the correlation between the standard and the random predictions:
222 the higher the correlation, the weaker the contribution or predictive power of the variable to explain
223 the species occurrence (Leroy et al., 2013). Ten randomizations were used for each variable with a
224 threshold of 0.1 to distinguish between strong and weak contributions (Leroy et al., 2013) which
225 corresponded to the mean importance for all variables (Capinha & Anastácio, 2010).

226

227 Effect of landscape metrics on the grey partridge occurrence

228 The relationship between landscape metrics and the probability of the occurrence of grey partridge
229 was assessed using the average response curves from GLMs calibrated on 100% of the data. The 95%
230 confidence intervals were calculated as a measure of the uncertainty for 100 GLM runs. The range of
231 habitat values selected by partridges were drawn based on the average cutoff calculated for each
232 period (Wilfried Thuiller, pers. comm., 2016). The cutoff is the threshold maximizing TSS and is
233 calculated for each model run under *biomod2* (Leroy et al., 2013; Wilfried Thuiller, pers. comm.,
234 2016).

235

236 Trends in the relation between partridge occurrence and landscape metrics

237 To test whether time (explanatory variable) had a significant effect on the contribution (response
238 variable) of landscape metrics, we used a generalized least squares (GLS) model using the *nlme*
239 package. To handle autocorrelation in our time series, we run an autocorrelation function on each
240 dependent variable to identify the time lag after which the non-autocorrelation assumption was
241 confirmed at 95% confidence level (Shumway & Stoffer, 2011). Then GLSs were implemented with an
242 autoregressive moving average (ARMA) term in which the moving average (MA) errors were
243 accounted for using the maximum time lag determined in the previous step. The lack of sequential
244 autocorrelation in the residuals was checked using the *acf* function. The 5-year moving average
245 windows allow a smoothing effect in the shape of the relationship between time and variable
246 contribution. Finally, we included a quadratic time term in the GLS models and used backward
247 stepwise selection procedure (Faraway, 2005).

248 The curves for each of four contiguous windows (1997-2001, 2002-2006, 2007-2011 and 2012-
249 2016) were also drawn for each landscape metric that both made a large contribution and changed
250 significantly with time.

251

252 Habitat suitability maps and trends in habitat quality

253 We forecasted habitat suitability maps for the periods 1998-2002 to 2013-2017 from the models
 254 fitted to the period 1997-2001 to assess how suitable habitats formerly selected by partridges have
 255 shifted over time. Habitat suitability was mapped as the probability of occurrence from an ensemble
 256 model, averaging all GLMs with TSS > 0.4 (Engler et al., 2011; Zhang et al., 2015), each one weighted
 257 by its TSS. Then, we calculated Schoener's D (Schoener, 1968 reviewed by Warren, Glor, Turelli, &
 258 Funk, 2008) as a measure of similarity in the geographical space between the habitat suitability maps
 259 of each period and the earliest one (1997-2001).

$$260 \quad D(p_X, p_Y) = 1 - \frac{1}{2} \sum_i |p_{X,i} - p_{Y,i}|$$

261 where $p_{X,i}$ and $p_{Y,i}$ represent the probabilities of occurrence of the grey partridge in the pixel i for the
 262 periods X and Y . The maps were then transformed into binary maps of suitable *versus* unsuitable
 263 areas, the threshold being the cutoff of the models calibrated on data of 1997-2001 (Leroy et al.,
 264 2013). The averaged value of habitat suitability index (i.e. the probability of occurrence) and the
 265 mean size of suitable habitat patches were calculated for each period.

266

267 **Results**

268 First, we investigated the key landscape metrics explaining the grey partridge occurrence over the
 269 study period (1997-2017), and their effect on grey partridge occurrence. Of the nine candidate
 270 explanatory variables, cereal density, distance to woodlands and distance to the nearest building
 271 were the metrics with the highest contributions when fitting to the aggregated dataset for 1997-2017
 272 (contributions >0.1, Fig. 2; Table S3). Most response curves were quadratic: moderate values of
 273 cereal density (25% to 65%) and distance to woodlands (300 m to 1310 m) were preferred by
 274 partridges while extreme values were avoided (Fig. 3). Partridges also preferred being more than 125
 275 m from a building (Fig. 3).

276 For the contiguous five-year periods, most of the metrics had similar contributions to those
277 for the whole dataset (Fig. 2; compare black and grey boxes), though the contribution of the distance
278 to buildings was below the 0.1 threshold and the contribution of the road density increased above
279 the 0.1 threshold (Fig. 2). The response curve for road density was also quadratic with a preference
280 for densities between 20 m/ha and 200 m/ha (high road densities were mainly in built-up areas) (Fig.
281 3).

282 Then, we performed a trend analysis to investigate whether the importance of the key
283 landscape metrics and their effect on grey partridge occurrence have changed with time. The trend
284 analysis of the 17 five-year moving windows showed that there were significant variations over time
285 in the contributions of some metrics (Table S4). For example the contribution of cereal density was
286 variable in the first few years and then increased in the last 15 years. This increase in contribution
287 was associated with a decrease of sightings in areas with low cereal density unselected by partridges
288 (13% of sightings in area with cereal density < 0.25 in 1997-2001; 7% in 2012-2016; Table S5). The
289 contribution of road density increased over the whole period with the selected range contracting
290 from 0-270 m/ha in 1997-2001 to 35-165 m/ha in 2012-2016 (Fig. 4, Table S6). Recently partridges
291 appeared to avoid woodlands and to buildings less, as the contributions of these metrics decreased
292 (Fig. 4, Table S4). Currently, partridges prefer areas closer to woodlands (distance to woodlands is
293 19.5% shorter) than at the start of the study period (820 m in 1997-2001 decreasing to 660 m in
294 2012-2016, Fig. 4, Table S6). This result is also consistent with raw numbers of partridge sightings
295 (15% of sightings at a distance to woodlands < 250 m in 1997-2001; 22% in 2012-2016; Table S5).
296 Partridges were less likely to avoid buildings in recent years than in 1997-2001 when they avoided
297 areas closer than 160 m to a building (Fig. 4, Table S6). In 1997-2001, 13% of sightings were collected
298 at a distance lower than 160 m to buildings, against 21% in 2012-2016 (Table S5). The contribution of
299 the size of crop patches decreased while that of hedgerow density increased, but both contributions
300 were small (Fig. S2, Table S4).

301 Finally, we assessed the trends in habitat suitability with time. Habitat suitability maps
302 calibrated on the first period (1997-2001) and forecast using the 1998-2002 to 2013-2017 metrics,
303 suggested a general decrease by about 26% in the mean size (from 26.4 ha in 1997-2001 to 19.6 ha in
304 2013-2017) and a slight decrease in the mean suitability index (from 0.696 in 1997-2001 to 0.682 in
305 2013-2017) of suitable patches for partridges (Fig. 5). Schoener's D statistic assessing the similarity of
306 the habitat suitability maps between each 5-year period and the first one decreased by 18.5% over
307 time (Fig. 6, Table S7). Even though the quality of our models remained relatively low (TSS= 0.42±0.03
308 for the seventeen 5-year periods, Table S3), it was high enough to be considered useful being above
309 the recognized threshold of 0.4 (Engler et al., 2011; Zhang et al., 2015).

310

311 **Discussion**

312 Despite many releases of captive-reared birds in the study area, the population of grey partridges has
313 suffered a drastic decline over the last 21 years. While we observed a general decrease in the size
314 and suitability index of suitable patches, our study showed that occurrence of partridges has changed
315 with landscape features.

316 Considering the overall 21-year period (1997-2017), the density of cereals, the distance to
317 woodlands and the distance to the nearest building were identified as the main contributors or key
318 drivers of grey partridge occurrence (Bellard et al., 2016; Wilson et al., 2013). Cereals is well known as
319 the main breeding cover selected by grey partridges (69 % of nests in Bro et al., 2013), associated
320 with high nesting success (Bro et al., 1998). However, the response curve shows saturation, indicating
321 a need for complementary habitats, for example rape for food (Birkan et al., 1992). High
322 contributions of distances to woodlands and buildings were expected because of avoidance of
323 carnivore reservoirs (Dudzinski, 1992; Reitz et al., 2002; Reitz & Mayot, 1999) and woodlands have
324 already been identified as the main driver of grey partridge distribution at local district scale
325 (Ronnenberg et al., 2016). For the four five-year contiguous periods the distance to buildings was less

326 important while road density was more important. Partridges avoided low road densities, as nesting
327 sites are frequently close to roads (25% of nests located in cereals, Bro et al., 2013), but they also
328 avoided high road densities, either because of predation risk (Reitz & Mayot, 1999) or disturbance by
329 traffic (Fahrig & Rytwinski, 2009). Although the population was mainly captive bred, this suggests that
330 the partridges showed patterns of habitat selection that were driven by well-known ecological
331 requirements.

332 An unexpected result is that there was a strong increase in the contribution of cereals to
333 explain the grey partridge occurrence over the past 15 years. As the cereal density has increased by
334 about 20% of the preexisting density observed in 1997 (Bretagnolle et al., 2018b), this cover has
335 become more widespread, and a subsequent decrease in the contribution of cereals might be
336 expected. The selection and high nesting success of cereals (Bro et al., 2013, 1998), associated with
337 the depletion of grey partridge densities may explain this result. The depletion would have been
338 higher in the low and unselected densities, as supported by the decreasing number of sightings in
339 areas providing low cereal densities. The other main result is the decreasing contributions of
340 distances to woodlands, buildings, on the partridge occurrence, associated with increasing
341 proportions of partridge sightings close to these predator-rich features. While these landscape
342 features have remained fairly stable over time, this suggest that partridges became less likely to
343 avoid woodlands and buildings (predator reservoirs) and roads (high exposure to predation) (Reitz &
344 Mayot, 1999), though they were expected to select the best quality habitats. Nonetheless, lower
345 avoidance of roads could also be partly explained by the decreasing partridge density associated with
346 the opportunistic nature of sightings, usually collected from roads. Such shifts in grey partridge
347 habitat preferences towards more risky habitats associated with lower survival expectancy have
348 already been described and explained by captive rearing of partridge and other galliformes, lacking
349 antipredator behavior (Rantanen, Buner, Riordan, Sotherton, & Macdonald, 2010a, 2010b; Sokos,
350 Birtsas, & Tsachalidis, 2008). Furthermore, captive-reared birds could also suffer from natal habitat

351 preference induction (Stamps & Swaisgood, 2007), encouraging them to select anthropogenic
352 features similar to those where they were reared. However, as habitat selection impairing fitness has
353 also been documented in wild grey partridges (Bro, Mayot, Corda, & Reitz, 2004) and other farmland
354 birds (e.g. the yellow wagtail *Motacilla flava* in Gilroy, Anderson, Vickery, Grice, & Sutherland, 2011),
355 there may be another explanation. This shift in habitat selection pattern could be linked to a
356 behavioral adjustment to the decreasing habitat quality and food availability. For instance, over the
357 last 30 years, seed availability has dropped faster in field cores than at field edges (Fried, Petit,
358 Dessaint, & Reboud, 2009). Partridges could, therefore avoid roads less, as roadside habitats may
359 provide more insect and seed food (Hopwood, 2008; von der Lippe, Bullock, Kowarik, Knopp, &
360 Wichmann, 2013) and higher seed abundance has already been linked to higher densities of farmland
361 birds, including grey partridge (Moorcroft, Whittingham, Bradbury, & Wilson, 2002). This hypothesis
362 could also explain the increase in the contribution of cereal density as the decrease in landscape
363 diversity would encourage partridges to prefer this cover which is associated with a high nesting
364 success rate (Bro et al., 2013, 1998). The continuous drop in habitat quality caused by agricultural
365 intensification, could have increased the concentration of prey and the predation pressure on the
366 remaining suitable patches (Aebischer & Ewald, 2012). This raises concern about low-density
367 populations, which may be particularly damaged as a result of a behaviorally mediated Allee effect:
368 there is no competition for space and individuals are free to select their preferred, though possibly
369 associated with lower survival, habitats (Kokko & Sutherland, 2001).

370

371 ***Implications for management***

372 The grey partridge study population, with a current density of around 1 male (or pair) per 400 ha,
373 may not be sustainable. Additionally, the observed changes in habitat selection towards more risky
374 habitats could impair the situation and may be exacerbated by releases of captive-reared birds,
375 documented to suffer deficiencies in antipredator behaviour, poor survival and breeding success

376 (Parish & Sotherton, 2007; Rantanen et al., 2010b). Therefore, initiatives releasing captive-reared
377 birds (about 250 birds per 1700 ha, the mean area of a local community) may actually precipitate,
378 rather than mitigate, the fate of local populations, since these naïve birds outnumber wild individuals
379 (Reitz, 2003; Sokos et al., 2008). Furthermore, these costly release programs, about €55k to €60k
380 each year in the LTSER (36 hunting associations × 250 birds × €6.5), have so far failed to help the
381 population recover, as numbers are still declining in the LTSER and the surrounding countryside.
382 Extrapolating to other gamebird species (€55k to €60k per year for red-legged partridges and €45k to
383 €50k for ring-necked pheasants) the costs of supplementing the local populations of gamebirds can
384 be estimated at €155k to €170k per year in our study area, with no perceivable improvement in
385 population sustainability.

386 This does not imply that reinforcement is an invalid strategy, since several conservation
387 programs would have sustainably increased partridge densities (Bro, 2016; Browne, Buner, &
388 Aebischer, 2009; Buner & Aebischer, 2008). These programs, however included supplementary
389 feeding, reestablishment of refuge covers and insect-rich habitats for chicks (set-asides, grassy strips
390 along field edges, field divisions, game covers), and nest protection or predation control when
391 needed to accelerate population recovery (Aebischer, 2009; Aebischer & Ewald, 2012; Bro, 2016). In
392 our study area, money saved by reducing by half the amount of captive-reared bird released (i.e. by
393 €80k) might be reallocated to create for example 270 ha of set-asides or wildlife covers, or a
394 maintenance of 40 km² (i.e. 1/5 of the cereal area) of stubble fields until the end of the chick rearing
395 period. In addition, the origin of the released birds was identified as a critical factor in success
396 whether the aim was game management or conservation (Fischer & Lindenmayer, 2000; Griffith,
397 Scott, Carpenter, & Reed, 1989). For instance, Sokos et al. (2008) reported a failure to re-establish a
398 pheasant population in a release program involving 3000 captive-reared birds, while the release of
399 1000 wild-caught individuals succeeded.

400 In the case of the grey partridge, we believe that we need to change from releasing captive-
401 reared gamebirds for 'put and take' shooting (Sokos et al., 2008), to conservation programs aiming to
402 restore self-sustaining populations. Efforts should be redirected towards habitat improvement
403 through selected agricultural practices, to greatly increase refuge covers, insects and seeds in the
404 landscape, with hunting restrictions to ensuring that the bird populations are self-sustaining, coupled
405 with releases of wild-caught or predator-trained birds (Sokos et al., 2008). Creating synergy between
406 all stakeholders, hunters, farmers and scientists, is, however, critical to achieve such integrated, local
407 biodiversity management.

408

409 **Authors' contributions**

410 VB set up the long-term partridge and land-cover monitoring; numerous fieldworkers supervised by
411 VB collected the data. OP, VB, MS and CH conceived the ideas and designed methodology; CH and OP
412 analyzed the data; CH, OP, VB and MS wrote the manuscript. All authors contributed to the drafts
413 and gave final approval for publication.

414

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421

422 **Data accessibility**

423 Partridge sightings and landscape metrics: OSF doi: [10.17605/OSF.IO/QJ237](https://doi.org/10.17605/OSF.IO/QJ237)

424

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- 613

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614 *Figure 1.*

615 *a) Location of the Long-Term Socio-Ecological Research (LTSER) platform “Zone Atelier Plaine & Val de*
616 *Sèvre” in France. Black dots inside the LTSER represent grey partridge sightings recorded from 1997 to*
617 *2017*

618 *b) Density of grey partridge opportunistic sightings (see Methods), from 1997 to 2017.*

619 *c) Density of cereals (time varying) and woodland (stable) from 1997 to 2017. Solid lines represent*
620 *significant trends from generalized least squares (GLS) model with autoregressive moving average*
621 *(see Table S1 for statistical details).*

622 *d) Average size of crop patches from 1997 to 2017 on the LTSER. Solid lines represent significant*
623 *trends from GLS models with autoregressive moving average.*

624 *e) Grey partridge sightings each year between 1997 and 2017 for each dataset (black: opportunistic*
625 *sightings; dark grey: point counts; light grey: point counts with call playback).*

626 *f) Distribution of grey partridge sightings recorded in each month of the year from 1997 to 2017*
627

628

629

629 *Figure 2. Contributions of landscape metrics to models calibrated on the whole 21-year period (black)*
630 *and cumulative contributions to models calibrated on the four contiguous five-year periods (1997-*
631 *2001, 2002-2006, 2007-2011, 2012-2016). Rape density was discarded from the analysis for the whole*
632 *21-year period as it was correlated with cereal density. The dashed line represents the threshold used*
633 *to distinguish the landscape metrics that contributed most to the model (Capinha & Anastácio, 2010;*
634 *Leroy et al., 2013).*

635

636

637 *Figure 3. Probability of occurrence of grey partridge as a function of the landscape metrics that*
638 *contributed most. Dashed lines represent the mean probability of occurrence below the cutoff, dotted*
639 *lines represent 95% confidence intervals, solid lines represent the range of values selected by grey*
640 *partridge (above the cutoff, see Methods).*

641

642

643 *Figure 4. Top: contributions (black dots) of landscape metrics in the 5-year moving window. Solid lines*
644 *show the trends from the GLS model with autoregressive moving average (see Table S4 for statistical*
645 *details). The dashed line represents the threshold used to distinguish the landscape metrics that*
646 *contributed most to the models (Capinha & Anastácio, 2010; Leroy et al., 2013). Error bars correspond*
647 *to the standard deviation of the contributions.*

648 *Bottom: Probability of occurrence of grey partridge as a function of the landscape metrics for the four*
649 *contiguous five-year periods (1997-2001, 2002-2006, 2007-2011, 2012-2016). Dashed lines represent*
650 *the mean probability of occurrence below the cutoff, dotted lines represent 95% confidence intervals,*
651 *solid lines represent the range of values selected by grey partridge (above the cutoff, see Methods).*

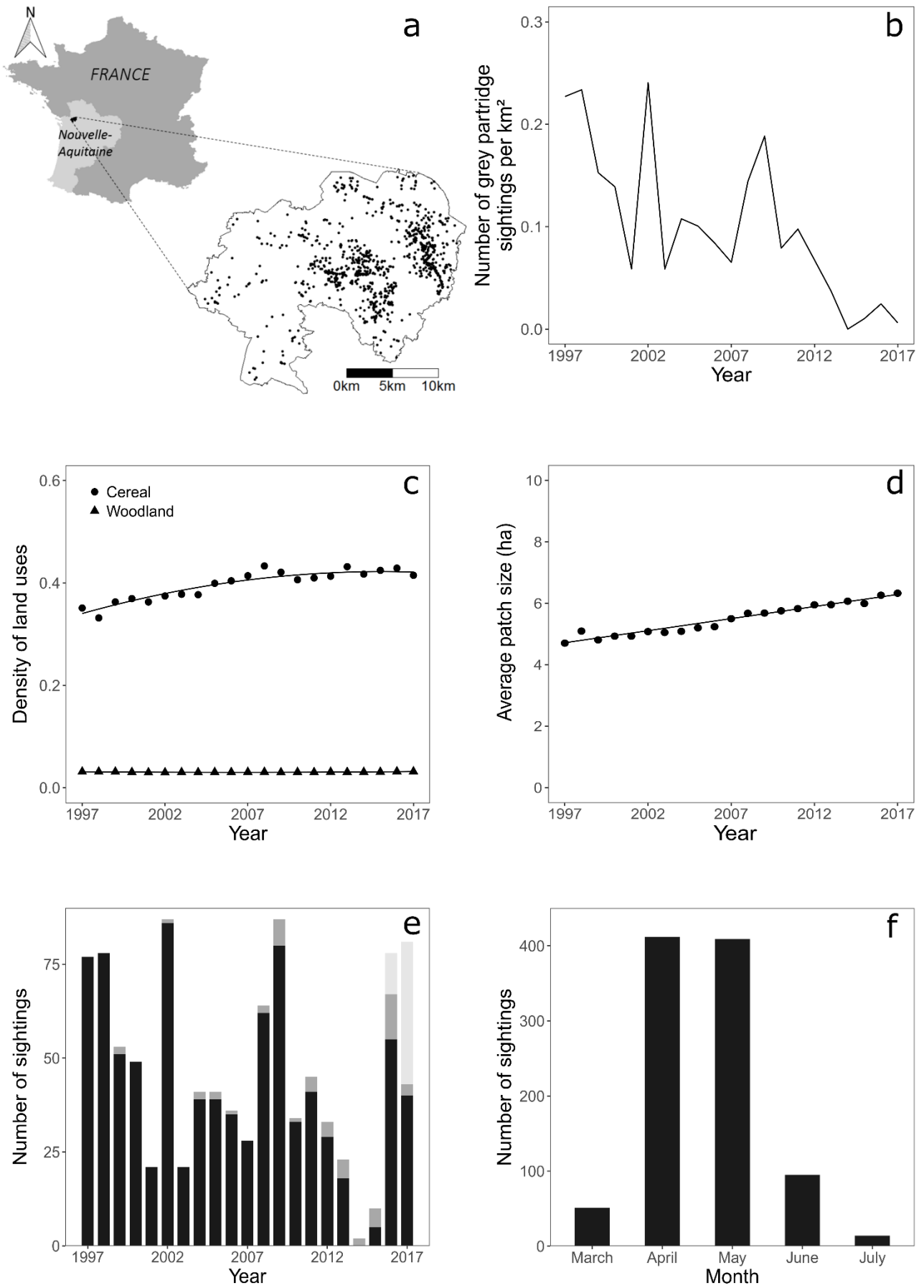
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653 *Figure 5. Predicted habitat suitability index of the LTSER for the four five-year contiguous periods. X*
654 *and Y axes are the coordinates (Lambert 93, EPSG:2154)*

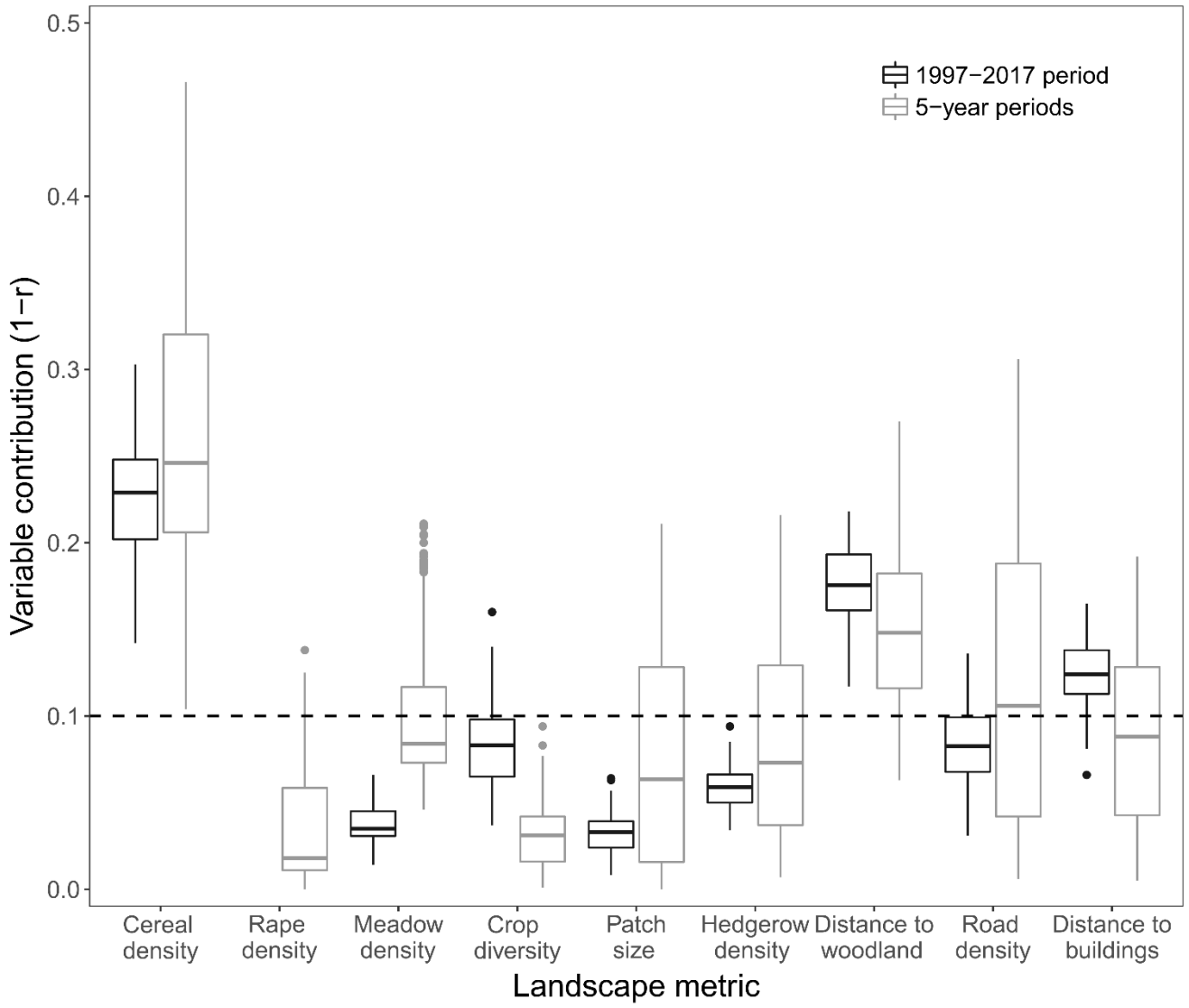
654

Habitat selection in grey partridge



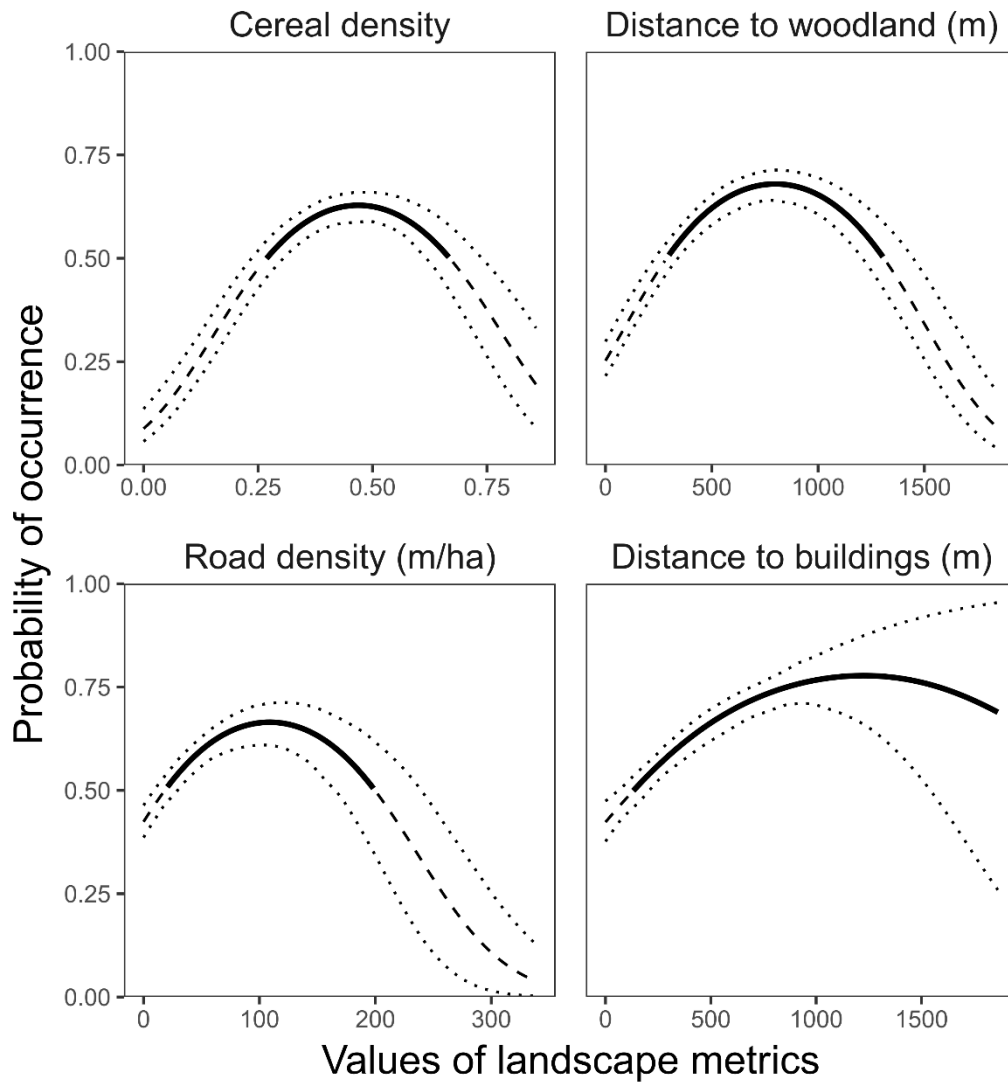
655
656 **Figure 1.**

Habitat selection in grey partridge



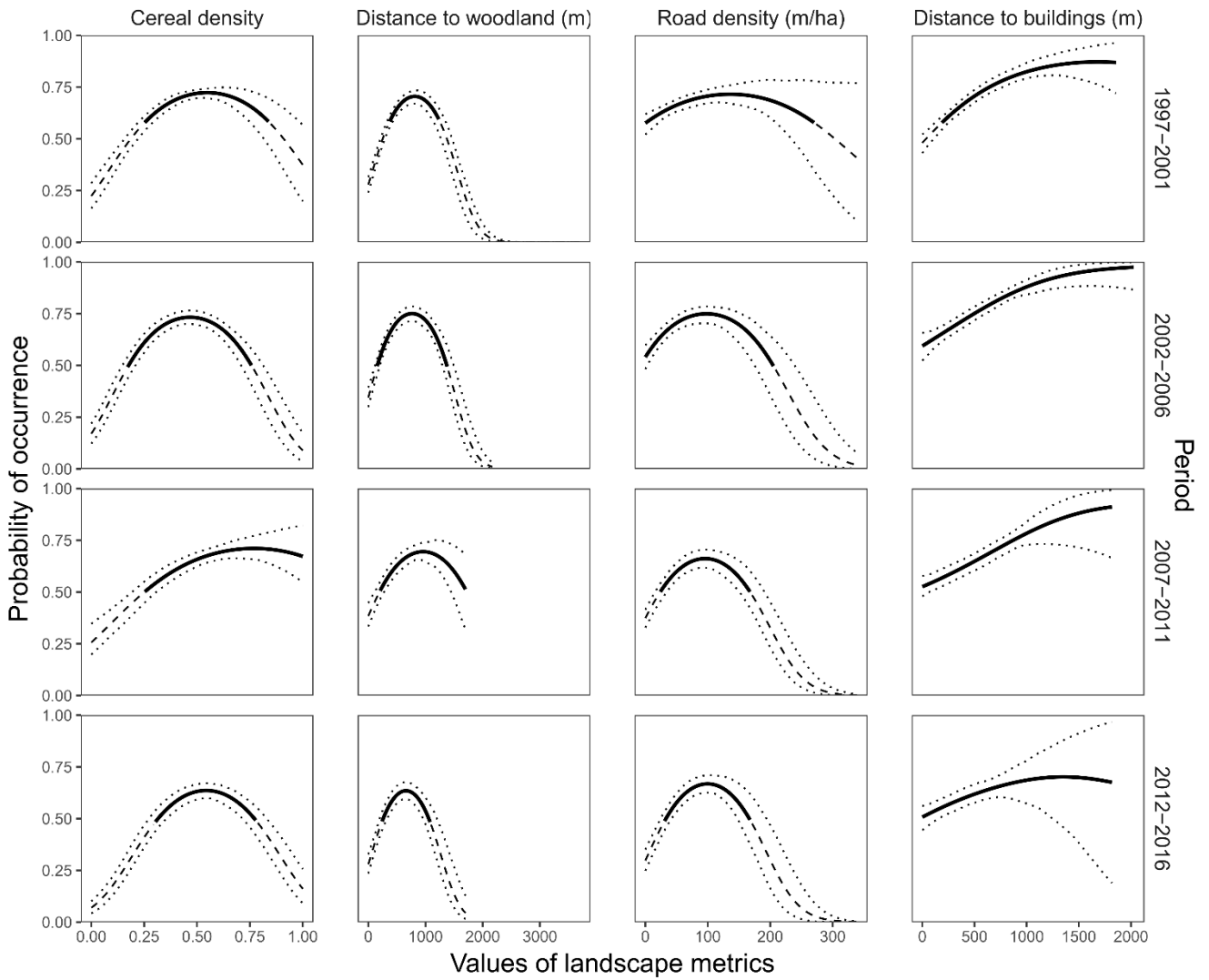
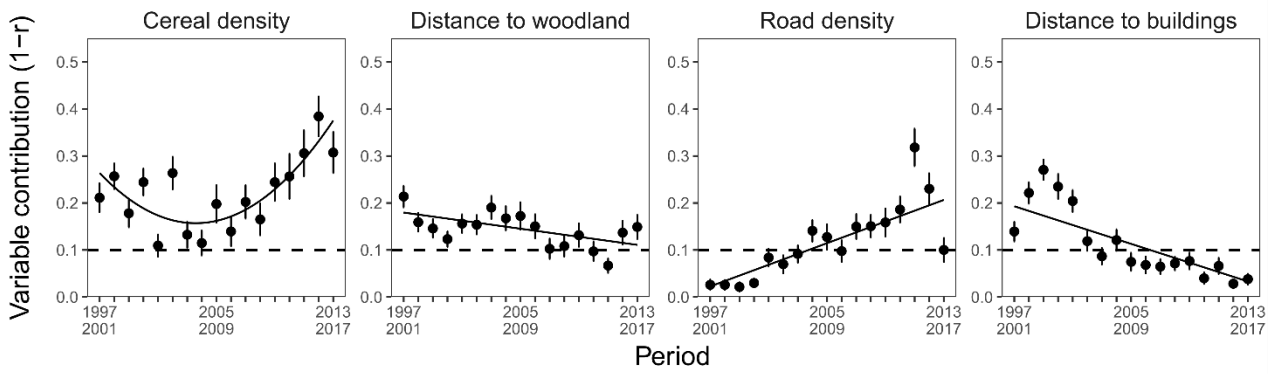
657
658 **Figure 2.**

Habitat selection in grey partridge



659
660 **Figure 3.**

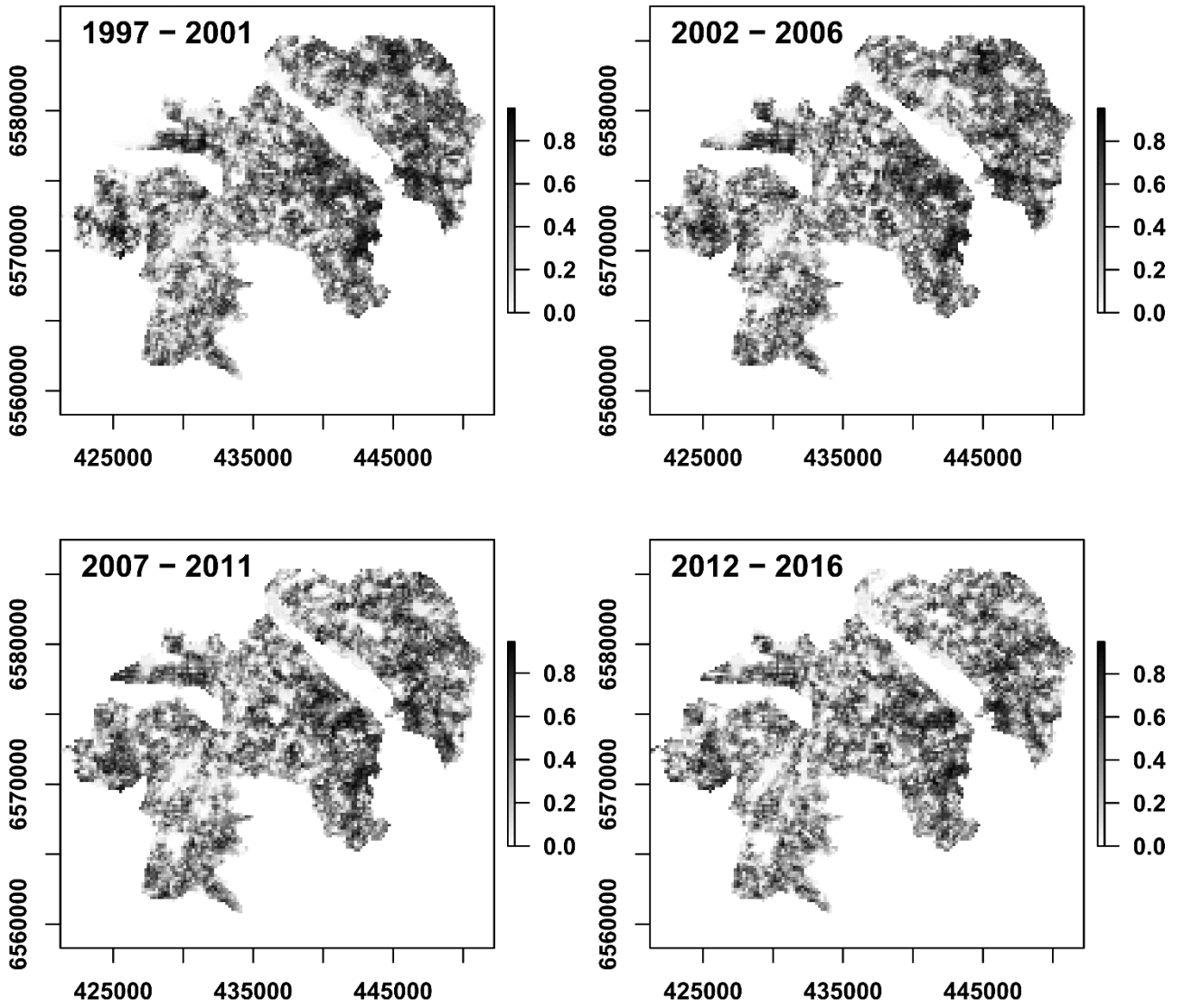
Habitat selection in grey partridge



661
662

Figure 4.

Habitat selection in grey partridge



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664 **Figure 5.**