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1 **Hedgerows interact with forests to shape the abundance of mesopredators and their predation**
2 **rate on eggs in farmland landscapes**

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4

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19

20 **Abstract**

21 Nest predation is the main cause of reproductive failure, particularly in ground-nesting birds on
22 farmlands. Understanding the links between nest predation and habitat change can help design
23 effective management schemes to constrain the negative impact of predation pressure on birds.
24 However, the mechanisms underlying the relationships between landscape attributes, predator
25 distribution, and nest predation are still unclear. Here, we use an experimental approach to examine
26 the effects of distance to the hedgerow as well as hedgerow and forest densities on the abundance
27 of major mesopredators of ground nests of our study area (i.e., corvids) and on the predation rate of
28 artificial ground nests (n=2576). We found evidence that landscape configuration influenced
29 predation patterns differently depending on the predator species. Nest predation by corvids was
30 more likely in homogeneous and open agricultural landscapes with a low density of forest and
31 hedgerows, whereas predation by other predators was more likely close to hedgerows. Nest
32 predation by corvids and the abundance of corvids also tended to be lower in landscapes dominated
33 by grasslands. Other variables such as road density and distance to human settlements had
34 contrasted effects on the likelihood of a nest being depredated by corvids, i.e., no effect with
35 proximity to human settlements and decreasing trend with road density. Altogether, our results
36 suggest that landscape features interact with mesopredator distribution and their predation rates of
37 ground nests. Therefore, from a conservation and management perspective, a heterogeneous
38 agricultural landscape that includes a mixture of crops associated with patches of forests,
39 hedgerows, and grasslands offering alternative food to generalist predators should contribute to
40 reducing ground-nesting bird predation.

41 **Keywords:** artificial nest; corvids; land use; landscape structure; road density; predator management

42 **1. Introduction**

43 Farmlands are complex mosaics of extensive crops mixed with semi-natural elements (Fahrig et al.,
44 2011; Martin et al., 2019; Sirami et al., 2019), that are used to sustain high levels of biodiversity.

45 However, over the second half of the twentieth century, such landscapes have profoundly changed
46 through agricultural intensification (García-Martín et al., 2021), which led to considerable shifts in
47 landscape structure, e.g., hedgerow network impoverishment and landscape homogenisation
48 (Benton et al., 2003; Gámez-Virués et al., 2015). Land management intensification has also affected
49 biodiversity and ecological processes (Allan et al., 2015; Emmerson et al., 2016; Newbold et al.,
50 2015), including food webs and predator-prey relationships (Manton et al., 2019; Rusch et al., 2016;
51 Shapira et al., 2008).

52 Agricultural intensification, together with top predator extirpation and game releases for hunting
53 purposes (Pringle et al., 2019), have contributed to triggering changes in the abundance of generalist
54 mesopredators (Roos et al., 2018; Terraube and Bretagnolle, 2018) and prey species dynamics
55 (Andrén, 1992a, 1995; Bayne and Hobson, 1997), though other factors are also involved in predation
56 rates (Kentie et al., 2015; Madden et al., 2015). Since top predators have not recovered enough in
57 most areas (Terraube and Bretagnolle, 2018), alternative methods have been established to mitigate
58 the impacts of mesopredators, such as lethal predator controls (trapping, shooting) or predator
59 exclusion. However, the effectiveness of lethal predator control in affecting predator demographic
60 parameters and enhancing prey species conservation has been questioned (Dinkins et al., 2016;
61 McMahon et al., 2020; Smith et al., 2010). Predator exclusion provides interesting results at a local
62 scale (Malpas et al., 2013; Melstrom and Horan, 2013), but remains difficult to apply at a broader
63 scale (Rickenbach et al., 2011). Landscape management has been suggested as a promising avenue
64 and has indeed shown positive effects (Dunn et al., 2016; Laidlaw et al., 2017), either by lowering the
65 predation success rate or by improving habitat quality by providing alternative food resources
66 (natural grasslands, hedges) for predators (Wilson et al., 2005).

67 In farmlands, studies have reported that predation shapes both nesting success and chick survival,
68 however, the effects of landscape attributes on predation patterns are still unclear (Kauffman et al.,
69 2007; Tewksbury et al., 2006), as is the interplay between habitat structure, predation risk, and
70 predator distribution (Chiavacci et al., 2018; Tewksbury et al., 2006; Van Der Vliet et al., 2008). Forest
71 density (Andrén, 1992; Small and Hunter, 1988), edges or hedgerows (Batáry and Báldi, 2004; Hinsley
72 and Bellamy, 2000), and anthropogenic attributes (e.g., roads) (Pescador and Peris, 2007; Silva et al.,
73 2019) affect nest predation dynamics both at a local and broader scale (Ellis et al., 2020). However,
74 habitat structure, predation risk, and predator community and distribution are interconnected,
75 making ecological mechanisms underlying predation dynamics hard to decipher, particularly in the
76 network of mesopredators and ground-nesting birds (Lahti, 2009). Several landscape attributes might
77 influence prey-predator interactions. Firstly, hedgerows can act as corridors, particularly for
78 mammalian predators (Graham et al., 2018; Pelletier-Guittier et al., 2020) and provide advantageous
79 perching/lookout positions for avian predators like corvids, presumably enhancing predation rates
80 close to edges. Furthermore, hedgerows might be attractive to predators because of their high prey
81 density and concealment, hence it also might increase predation rates close to hedgerows. However,
82 how hedgerows interact with other landscape attributes, such as forest density and crops is unclear.
83 Secondly, forests and land use cover might also determine the availability of prey for generalist
84 predators. Considering the landscape structure context, predictions of hedgerow effects might be
85 less straightforward when, for instance, the availability of food resources is similar in hedgerows to
86 some land uses. Thirdly, in open farmlands with rare forest patches, forest patches might lead to a
87 spill-over of generalist predators into the adjacent farmland matrix, hence increasing nest predation
88 in such mixed landscapes (Andrén, 1995). Fourthly, anthropogenic features might also shape
89 predation patterns through their effect on mesopredator abundance. For instance, roads and
90 human-supplied food resources may attract opportunistic vertebrate species that actively search for
91 carrion along roads or generalist species adapted to living with humans. Finally, nest predator
92 communities differ in response to landscape attributes (Andrén, 1992; Chalfoun et al., 2002).

93 Although the social status of predators is important for assessing the impact of avian predators on
94 nest predation dynamics (Bravo et al., 2020), whether nest predators respond to landscape attributes
95 differently depending on social status has received little attention.

96 In this study, we designed an experimental set-up with artificial ground nests (n=2576) in an
97 intensive agricultural landscape. Previous results in our study area have shown that corvids were the
98 main predators of ground nests (Bravo et al., 2020). To quantify the predation rate on ground nests,
99 accounting for both the abundance of mesopredators and landscape features, we first investigated
100 how the distance to hedgerow, hedgerow density, and forest density affected the probability of a
101 nest being depredated. While land uses and anthropogenic features are expected to affect predation
102 patterns (i.e., by improving or limiting the availability of food resources for predators), we mainly
103 hypothesised that the hedgerow effect on predation rate would differ depending on the habitat use
104 and density of potential predators (Andrén, 1995). Proximity to hedgerows is expected to affect
105 avian predators, such as corvids, differently to other predators such as mammals. Since predation
106 patterns should be affected by the availability of forest patches or landscape connectivity (e.g.,
107 density of hedgerow network), we hypothesised that the predation rate would decrease as the
108 density of hedgerows and forests increases (Andrén, 1992). Then we assessed how the abundance of
109 mesopredators changed with the same landscape attributes (hedgerow and forest density). Since
110 reproductive status (breeder or not) and land use (i.e., as a proxy of food resources) may affect the
111 distribution of predators, we hypothesised that the abundance of nest predators (e.g., corvids) would
112 increase in homogeneous landscapes with low hedgerow and forest density (Andrén,1995). Finally, if
113 landscape shapes the distribution of predators and thus their predation rates on ground nests, the
114 relationship between landscape variables (mainly hedgerows and forest) and the probability of a nest
115 being depredated is expected to show a pattern similar to the one between landscape variables and
116 the abundance of mesopredators. Prey-predator systems are complex, and as is the case in many
117 ecological systems (Díaz and Concepción, 2016; Fernández et al., 2002), non-linear relationships
118 between predictors and response variables are expected. For this reason, we have considered

119 quadratic effects to capture potential non-linear relationships between landscape predictors and egg
120 predation and corvid abundance.

121

122 **Methods**

123 **1.1. Study Area**

124 The study was carried out in the LTSER 'Zone Atelier Plaine & Val de Sèvre', central Western France
125 (46°15N, 0°30W, Fig. 1), which comprises 450 km² of intensive agriculture, mostly dedicated to cereal
126 production (see (Bretagnolle et al., 2018) for a general description of the site). The area is
127 characterised by an open farmland landscape, almost flat (altitude 40 to 100 m asl) with a network of
128 hedgerows (that is, 'bocage') and small forest patches (Fig. 1). The hedgerows are generally 2 to 5 m
129 high and 1 to 10 m wide, with hawthorns (*Crataegus monogyna*), blackthorns (*Prunus spinosa*), and
130 common blackberries (*Rubus fruticosus*) as the main components. The most common crops are
131 wheat (33.8%), meadows (13.5%), corn (9.6%), sunflower (10.4%), oilseed rape (8.3%), and pea (2%).
132 The community of mesopredators includes raptors like harriers (*Circus pygargus*, *C. cyaneus*, and *C.*
133 *aeruginosus*), corvids like carrion crows (*Corvus corone*), Eurasian magpies (*Pica pica*), western
134 jackdaws (*C. monedula*), rooks (*C. frugilegus*) and Eurasian jays (*Garrulus glandarius*), and small
135 carnivores like red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), weasels (*Mustela nivalis*) and
136 domestic cats (*Felix catus*) (Bravo et al., 2022). The study area is an important breeding site for
137 protected bird species and game bird species. The presence of many species covered by the EU Birds
138 Directive led to the designation of a NATURA 2000 site in 2004 (FR5412007) on c. half of the LTSER.

139 **1.2. Predation experiment**

140 We monitored 2576 artificial nests set up at 112 sampling points during three breeding seasons,
141 2017-2019. The experimental design has been fully detailed in Bravo et al. (2022). A sampling point
142 consisted of a given location, at which several nests were placed at 30 m intervals along transects

143 (Fig. 1B). The sampling points were selected with a stratified scheme, according to the hedgerow
144 density and the forest fragments, in order to span a maximum range of each of these elements
145 across sampling points, while maintaining as low as possible paired correlations between these
146 elements. In 2017 and 2018, two transects per sampling point were set in two adjacent fields while,
147 in 2019, only one transect was set. Although the number of transects per sampling site differed in the
148 different years, we did not detect any spatial autocorrelation. The average distance (\pm SD) between
149 transects in 2017 and 2018 was 129.4 ± 52.91 m (range 52.16 - 355.71 m). Transects were set parallel
150 to the hedgerow, randomly at one of either four distances from the hedgerow (one distance per
151 sampling point): 10 m, 30 m, 50 m, and 70 m.

152 Nests consisted of eggs fabricated from off-white nontoxic odourless plasticine (J. Herbin plastiline,
153 Chelles, France). Each nest was formed as a shallow depression in the soil and contained two
154 identical plasticine eggs fixed by a thin wire and a nail in the ground to prevent predators from
155 carrying them away. Nest location was recorded by GPS position, no markers were placed.

156 Nests were set up weekly from 26th March to 19th June each year, allowing detailed analysis of
157 seasonal effects. Nest location was moved by at least 100 m from the location used in previous years
158 to avoid a memory effect. Nests were exposed to predators for 7 consecutive days in 2017 and 15
159 days in 2018 and 2019. This time allows to mimic the egg-laying period (when individuals leave their
160 nests open and are not incubating the eggs), which varies from 2 to 7 days for little bustard or
161 Montagu's harrier and is up to 15 days for partridges, three ground nesting birds typical of our
162 landscapes. As (i) the time of nest exposition varied among years and daily survival rates (DSR) were
163 not constant with time showing a quadratic pattern throughout the experiment (Appendix 1) and (ii)
164 our previous study showed that the nest halftime was 3 days on average (Bravo et al., 2022), we used
165 nest predation recorded on day 3 as a standardised measure of predation rate to control for the time
166 effect on the predation rate.

167 We deployed several egg types per sampling point to simulate predation rates by different predators
168 (Fig. 1B). We used three categories of egg sizes: large (5 x 3 cm), medium (3.5 x 2.5 cm), and small
169 (2.5 x 1.5 cm) and three colours (white-off, light green, and dark green). In 2017, four nest types
170 were deployed per sampling point: large white, small white, large light green, and small light green.
171 In 2018 and 2019, five nest types were deployed per sampling point: large white, small white, large
172 dark green, small dark green, and medium light green (see Appendix 2).

173 We considered nests to be depredated when one of the eggs had been damaged. Predator species
174 were identified by tooth and bill imprints in plasticine eggs (see Bravo et al. (2020)). Predator species
175 were identified as corvids or other species, such as mammals, small mammals, and raptors. Nests
176 destroyed by farming practices (n=21) were removed from the analyses.

177 **1.3. Estimating corvid abundance**

178 Corvid abundance (carrion crow and magpie) was estimated during the breeding season of the three
179 years (2017-2019) at each sampling point (n = 112). We tried to set point counts as close as possible
180 to nests, with mean (\pm SD) distances between point count and artificial nest location being $145.4 \pm$
181 120.7 m. Corvids were counted using 10-minute duration point counts repeated four times per
182 breeding season, at about 2-week intervals, spread from 29th March to 19th June each year. In each
183 visit, all auditory and visual contacts, their accurate location, and the behaviour of every single corvid
184 individual were recorded within a 300-m radius (i.e., 28.3 ha) around the observer. The minimum
185 territory size of a magpie is 2.53 ha (Baeyens, 1981) and 9 ha for a carrion crow (Yom-Tov, 1974).
186 Surveys were carried out within 4 h of sunrise while avoiding rainy or strong wind conditions
187 (Luginbuhl et al., 2001) . We repeated counts to discriminate territorial breeders from non-breeders
188 in each sampling point. The presence of territorial breeders was determined using a combination of
189 proxies. Firstly, the nests (whether active or inactive) were located in early spring (before the bud
190 burst, typically early March). Secondly, corvid behaviour was used as a proxy to indicate breeding
191 and territorial behaviour, such as bringing nest material, feeding, and territorial defense against

192 other corvids, alarm calls, and attacking raptors (Röell and Bossema, 1982; Tapper et al., 1996). And
193 thirdly, by analysing the four samples per point: if a pair was observed at least in 2 out of 4 counts, it
194 was assumed to be a territorial pair. The absence of a territorial pair/breeder was concluded
195 otherwise, i.e., if no nest had been observed, no breeding or territorial behaviour had been observed
196 in any of the four samples, and no pair was seen twice. Then, the total number of pairs per sampling
197 point was obtained, and the abundance of non-breeders (floaters) was determined as the maximum
198 number of corvids recorded on a given point minus the number of breeders.

199

200 **1.4. Landscape Variables**

201 Around each artificial nest and point count, we assessed the following landscape variables: i)
202 hedgerow density, forest density, and distance to the closest hedgerow as proxies of landscape
203 structure, ii) the proportion of different land uses (i.e., cereals, grasslands, spring crops, oilseed rape
204 and others, see below) as a proxy of alternative food for mesopredators, for instance, cereal crops
205 harbour fewer insects than others land uses (Díaz and Tellería, 1994), and iii) anthropogenic variables
206 such as distance to human settlements and road density (see Table 1 for details). Landscape variables
207 were quantified, from LTSER land cover monitoring (see (Bretagnolle et al., 2018)) and the database
208 of the Institut National de l'Information Géographique et Forestière (BD TOPO®). We used QGis
209 (version 3.4.12). We selected a 300 m buffer from each artificial nest and from each point count to
210 calculate the landscape variables since other buffer sizes (i.e., 100, 200, 400, and 500 m) led to lower
211 statistical support in the models investigating corvid predation or corvid abundance (see Appendix 3).

212 Given that hedgerow density might depend on the width of the hedgerow and hedgerow width is
213 quite variable in our study area, hedgerow density was defined as the surface (m^2/ha) of tree lines
214 forming a contiguous network across the farmed landscapes within the 300 m buffers. Polygons (and
215 thus hedgerow surfaces) were created from the tree lines and width of hedgerows, which varied

216 from 5m to 20 m wide. The forest density was defined as the surface of forest (m² / ha) patched
217 within the 300 m buffers.

218 Within the 300 m buffers, we extracted five types of land use according to the type and structure of
219 vegetation: cereals (mainly wheat), grasslands (meadows), spring crops (sunflowers and corns),
220 oilseed rape and other crops (such as ryegrass, wax, peas, and lens). As proportions of land uses were
221 correlated, we ran a Principal Component Analysis (PCA) to extract two uncorrelated synthetic
222 variables. PCA was conducted separately for predation and corvid abundance, and we extracted the
223 first two principal components as they accounted for 58.7% and 56.3% of the total variances,
224 respectively (see Appendix 4 for details). Loadings related to land uses indicated that i) when PC1
225 increased, the proportions of cereal crops increased in the landscape whereas spring crops and
226 grasslands decreased and ii) when PC2 increased, the proportions of spring crops increased whereas
227 grasslands decreased (Appendix 4).

228 Two variables were assessed as proxies of human disturbances: the distance (m) between the
229 experimental nest or the point count location and the nearest human settlement (i.e., houses,
230 industrial and agricultural buildings); and road density as the total length (m/ha) of paved roads
231 (motorway, national, departmental and communal roads) within the 300 m buffer.

232 We also accounted for how a specific crop type in the immediate vicinity of the nest influenced the
233 predation rate (hereafter, crop type; Bravo et al., 2022). For this, crop types were regrouped
234 according to vegetation type and structure as follows: cereals (mainly wheat and barley), grasslands
235 (meadows and alfalfa), spring crops (sown in late February and after, including mainly sunflower and
236 corn), and other crops (oilseed rape, ryegrass, wax, peas, and lens).

237 **1.5. Statistical Analysis**

238 **1.5.1. Predation Rates**

239 First, we investigated the relationship between landscape structure and the probability of a nest
240 being depredated (i.e., on day 3) using generalised linear mixed-effects models (GLMM) with a

241 binomial error distribution (logit link function) including distance to hedgerow, hedgerow density,
242 and forest density (all standardised), and all two-way interactions as predictors. As predictors might
243 affect the probability of predation in a non-linear way, we included their quadratic term. We also
244 included the two axes of the PCA that describe the proportion of land uses surrounding the
245 experimental nest location and their two-way interactions with the predictors of landscape structure
246 cited above. As crop type in which the nests were located may also affect the predation probability
247 (Bravo et al., 2022), crop type (with four levels, cereal, grassland, spring crop, and others) and its
248 two-way interactions with distance to hedgerow were included as predictors. To account for a
249 possible temporal effect in our models, year and julian day were also included. In a last step, to
250 investigate whether anthropogenic variables affected the relationship between landscape structure
251 and probability of nest predation, we run a model including road density and distance to human
252 settlements and their two-way interactions with the predictors of landscape structure (i.e., hedgerow
253 density, forest density and distance to hedgerow. We run separate models with predation carried
254 out by corvids (i.e., the main mesopredators of depredating nests) and other predators (i.e.,
255 mammals and raptors).

256 Potential confounding factors were present in our experimental design. First, since we showed that
257 egg types affected the probability of a nest being depredated in a previous study (Bravo et al., 2022),
258 this variable was also included as a random factor (with seven levels, large white, small white, large
259 dark green, small dark green, large light green, medium light green, and small light green). And
260 second, to account for the spatial structure of our data set, we included the transect id, nested in the
261 sampling point, as a random factor. Moran's I correlograms from the residuals of models using
262 'pgirmess' package showed the lack of spatial autocorrelation between experimental nests (Appendix
263 6).

264 **2.5.2. Abundance of corvids**

265 We analysed the effects of the same landscape parameters on corvid abundance, with similar
266 procedures and structured models. The first model included standardised landscape structure
267 variables (hedgerow density, forest density, their quadratic terms, and the two-way interaction as
268 predictors) using a generalised linear model (GLM) with Poisson error distribution (logit link
269 function). Land use proportion around the sampling point was then included with the first two PCA
270 axes (Appendix 4) and the two-way interactions between PCA and landscape structure. Then
271 anthropogenic variables (road density and distance to human settlements) were added. We run
272 models on the abundance of corvid breeders and floaters separately.

273 Corvid abundance varied significantly between years, both in breeders ($\chi^2 = 32.60$, $df = 2$, $p < 0.01$)
274 and floaters ($\chi^2 = 33.04$, $df = 2$, $p < 0.01$; see Appendix 5 for details). As the effect of year on corvid
275 abundance was not the focus of this article, we summed the sightings of individuals observed over
276 the three years. In this way, we gave greater weight to sampling points where corvids were observed
277 during the 3 years in the same area. We checked for the lack of spatial autocorrelation in the model
278 residuals using Moran's I correlograms (Appendix 6).

279

280 **2.5.3. Relationship between corvid predation and corvid abundance**

281 To investigate the relationship between corvid predation and corvid abundance, we run the first
282 model of corvid predation which included landscape variables as predictors (i.e., distance to
283 hedgerow, hedgerow density, forest density, their quadratic terms, and the two-way interaction, PCA
284 axes and crop type). This model was then compared with a model now including, in addition to
285 previous variables, corvid breeder abundance and another one including corvid floater abundance. If
286 landscape effects on nest predation were due to landscape effect on predator abundance, we predict
287 that the effect size (i.e., Odds ratio) of these landscape effects would lose significance when corvid
288 abundance is included in the models (Díaz et al., 2013).

289 For all models, we used 95% confidence intervals (CI) to investigate the significance of factors on the
290 probabilities of a nest being depredated and corvid abundance. We considered that there was not a
291 consistent effect when 95% CI overlapped the zero value. We used the package 'lme4' to run GLMM
292 (Bates et al., 2015). The coefficients of the graphs were extracted from the minimal model including
293 only significant predictors. All models were tested using R version 4.0.3 (R Core Team, 2021).

294

295 **3. Results**

296

297 From the experimental nests (n = 2576), 16.28 % were depredated (n = 416) during the 3-day period
298 with 84.4% of nests depredated by corvids and 14.9% by other predators (mammals and raptors).

299

300 **3.1. Effects of landscape features on predation rates**

301 The effect of distance to the hedgerow on the probability of a nest being depredated by corvids
302 varied significantly with the crop type. Corvid predation decreased with distance to hedgerows in
303 nests located in spring crops. In contrast, no significant effect of distance effect was observed for
304 nests located in cereal crops (Fig. 2A). Hedgerow and forest density also affected the corvid
305 predation rate in a complex quadratic manner (Table 2). The corvid predation rate was minimal (3-
306 5%) at medium-high hedgerow density (i.e., 600 - 1200 m²/ha) with forests being either absent or
307 highly present (Fig. 3). The probability of predation by other predators was highest when closest to
308 the hedgerow regardless the crop type (Fig. 2B, Table 2), while neither the hedgerow nor the forest
309 density affected this probability (Table 2B). Crop type did not affect predation probability by other
310 predators. Furthermore, the probability of corvid predation decreased by 45% during breeding
311 season (i.e., julian day), whereas predation by others tended to increase slightly with julian day
312 (Table 2, Appendix 5: Fig. S6). Therefore, predator type (i.e., corvids vs. non-corvids) was crucial in
313 understanding the effects of landscape structure on the predation rate of ground nests.

314 Corvid predation rate decreased as the proportion of cereal crops (i.e., PC1) increased from 0 to 0.8
315 in the landscape (Fig. 4). However, this effect depended on the crop type. Specifically, it decreased by
316 50% when the nest was located in spring crops, but remained unchanged in nests located in cereal
317 crops. Corvid predation rate was not influenced by the proportion of grasslands (i.e., PC2) (Table 2).
318 Conversely, the nest predation by other predators was not affected by either of the two PCA axes
319 (Table 2). Finally, the probability of corvid predation tended to decreased by 30% with an increase in
320 road density from 20 to 60 m/ha (Estimate \pm SE=-0.39 \pm 0.24; 95% CI = -0.90 — 0.08) but it did not
321 change with distance to human settlements (-0.23 \pm 0.26; 95% CI = -0.74 — 0.29). Road density and
322 distance to human settlements did not affect nest predation by other predators (-0.45 \pm 0.46; 95% CI
323 = -1.36 — 0.45; 0.10 \pm 0.18; 95% CI = -0.24 — 0.45, respectively).

324 **3.2. Effects of landscape features on corvid abundance**

325 The mean number of territorial corvid breeders was 2.41 individuals (\pm 0.84, range 0-6). They were
326 observed in 42.0-76.8% (depending on the year) of the sampling points (Appendix 5). The mean
327 number of corvid floaters was 3.81 individuals (\pm 6.77 individuals, range 0-58). They were observed at
328 67.9-81.3% of the sampling points. Considering the sum of corvid individuals over the three years,
329 the mean of territorial corvid breeders was 4.7 individuals (\pm 2.23, range 0-10) and of floaters was
330 8.34 individuals (\pm 10.62, range 0-62). Territorial corvid breeders and corvid floaters were present in
331 89.3% and 99.1% of sampling, respectively (Appendix 2).

332 The abundance of corvid breeders and floaters varied significantly with forest and hedgerow
333 densities in a complex way as effects were quadratic and sometimes interacting (Table 3). The
334 clearest signal was observed in corvid floaters with more individuals in poor hedgerow/forested
335 landscapes (Fig. 5B). The abundance of floaters was mainly affected by hedgerow density, with a
336 strong decrease from 25 to 10 individuals on average when hedgerow density increased from 200 to
337 1200 m²/ha (Fig. 5B). In contrast, the abundance of corvid breeders showed a quadratic relationship
338 with forest density (Table 3A), similarly to the probability of corvid predation. The number of

339 breeders was low (i.e., 2 individuals or 1 pair) at high forest density (i.e., 500 m²/ha), and increased
340 to reach 4 individuals (or 2 pairs) when there were no forest patches in the landscape and at 600
341 m²/ha of hedgerow density. The abundance of breeders was very similar to the probability of corvid
342 predation being maximal (i.e., 6 individuals or 3 pairs) when the forest density was around 300 m²/ha
343 and there were no or many edges (Fig. 5A).

344 The abundance of corvid breeders was not affected by the proportion of land uses, conversely to
345 corvid floater abundance, which responded strongly and negatively to the proportion of cereal crops
346 (i.e., PC1), and positively to the proportion of spring crops (i.e., PC2; Table 3B, Appendix 7: Fig. S9).

347 The two interactions PC1 × hedgerow density and PC2 × forest density significantly affected corvid
348 floater abundance (Table 3B). The abundance of corvid floaters decreased with hedgerow density
349 when there were no cereals in the area, while the effect of hedgerow density vanished when the
350 landscape was dominated by cereals (Appendix 7: Fig. S10). A similar pattern was found with forest
351 density and spring crops (Fig. S10).

352 The road density and the distance to human settlements did not affect the abundance of corvid
353 breeders (Estimate ± SE = -0.01 ± 0.06; CI 95% = -0.14 — 0.12; -0.09 ± 0.08; -0.25 — 0.07,
354 respectively), but affected the abundance of floaters (-0.32 ± 0.05; -0.42 — -0.23; -0.13 ± 0.06; -0.25
355 — -0.02, respectively). Considering the effect of the interaction between road density and hedgerow
356 density (0.35 ± 0.05; 0.25 — 0.46), the abundance of corvid floaters decreased with hedgerow
357 density when the road density was low and did not vary with hedgerow density when the road
358 density was high (Appendix 7: Fig. S11). Considering the effect of the interaction between road
359 density and forest density (-0.19 ± 0.06; -0.31 — -0.07), the abundance of corvid floaters increased
360 with forest density when the road density was low and did not change with forest density when the
361 road density was high (Fig. S11). To conclude, many floaters were observed in areas with few roads
362 and edges and many forest patches (Fig. S11).

363 **3.3. Relationship between corvid abundance and predation rates**

364 Corvid predation increased with corvid breeder abundance (Estimate \pm SE = 0.23 ± 0.05 ; CI 95% =
365 $0.13 - 0.32$, Appendix 8, Table S6), and did not with corvid floater abundance (0.00 ± 0.01 ; CI 95% = -
366 $0.02 - 0.03$, Table S6). When corvid breeder abundance was included in the model of corvid
367 predation, hedgerow density was no longer associated with corvid predation rate on eggs ($-0.26 \pm$
368 0.14 ; CI 95% = $-0.55 - 0.02$, Table S6). Consequently, corvid breeder abundance was associated with
369 the effect of hedgerow density on corvid predation. Conversely, distance to hedgerow and PC1
370 remained associated with corvid predation since their odd ratios did not change much (Table S6).
371 Finally, the model including corvid breeder abundance better explained the variation of corvid
372 predation (AIC=1603.51) than the model with corvid floater abundance (AIC=1623.34) or the model
373 including only landscape variables without corvid abundance (AIC=1621.34). Altogether, our results
374 suggest that hedgerow density was a decisive driver shaping the abundance of corvid breeders in our
375 study area and corvid predation rates of ground nests.

376 **4. Discussion**

377 At first sight, the use of artificial nests might appear to be limiting when examining the spatial
378 variation of the predation rate, as they do not allow actual values to be extracted from wild
379 conditions (Major and Kendal, 1996; Moore and Robinson, 2004). For instance, plasticine eggs may
380 prevent predation due to their artificial scent, particularly in mammals. In our study area, corvids
381 were the main nest predator, even when artificial nests were baited with natural eggs (Bravo et al.,
382 2020). While we acknowledge the potential influence of odour associated with plasticine eggs, our
383 results suggested that this effect might be negligible. Moreover, when standardised, the use of
384 artificial nests has proven to be an efficient method for comparing predation patterns across
385 different landscape attributes, hence assessing relative predation estimates rather than raw
386 estimates. Artificial nests are a powerful and non-intrusive methodology allowing a large number of
387 replicates.

388 Although the proximity of edges has largely been reported to shape the predation risk of forest birds
389 (Andrén, 1995; Batáry and Báldi, 2004), the effect of landscape on the predation risk of ground-
390 nesting species in open habitats remains unclear (Kaasiku et al., 2022; Lampila et al., 2005). Our
391 study provides evidence that the farmland landscape configuration shapes both the abundance of
392 mesopredators such as corvids and their predation rates on ground nests. Unlike corvid floaters, the
393 abundance of corvid breeders (predicted mainly by hedgerow and forest densities), explained the
394 variation of the ground nest predation rate by corvids. Indeed, variations in the abundance of corvid
395 breeders and variations in nest predation rate by corvids were explained by similar landscape
396 features, with the same slopes and signs. Therefore, our findings reveal that the predation rate by
397 mesopredators in our study area is mainly driven by the effects of landscape structure, showing an
398 effect of hedgerow and forest densities on the abundance of corvid breeders.

399

400 **4.1. Effects of edge and forest**

401 The predation rate was expected to increase when nests were close to hedgerows as mesopredators
402 are known to increase their activity at habitat edges (Batáry and Báldi, 2004; Kaasiku et al., 2022).
403 Our results supported this hypothesis, indicating that nest predators responded in different ways to
404 edge proximity (Krüger et al., 2018; Lahti, 2001). Predation by other predators was consistently
405 higher when closest to the hedgerow, regardless of the crop type, suggesting that hedgerows might
406 play a role as corridors for predators such as mammals. However, in the case of corvid predation, the
407 influence of edge proximity varied depending on the crop type in which the nests were located.
408 Corvid predation was higher close to hedgerows when nests were in spring crops, whereas no
409 significant effect of distance to hedgerows was observed for nests in cereal crops. This result
410 suggests that the nest concealment provided by vegetation structure might be key for the nest
411 predation by corvid in the proximity of hedgerows. Several studies failed to detect edge effects on
412 nest predation in open landscapes (Donovan et al., 1997; Kaasiku et al., 2022) as it depends on

413 landscape configuration, not only on the distance to edge per se (Batáry and Báldi, 2004; Chalfoun et
414 al., 2002; Ludwig et al., 2012). Understanding the edge effect on predation patterns requires
415 considering the landscape structure, including crop types, the availability of forest patches, and
416 landscape connectivity (Chiavacci et al., 2018).

417 When hedges are lacking, landscapes with a density of forest around 100-200 m²/ha (i.e., only 2-3%
418 of the surface) had the highest probability of the nest being depredated by corvids. This pattern is
419 supported by other studies that found higher densities of corvids (e.g., hooded crows *Corvus cornix*)
420 in mixed landscapes (Smedshaug et al., 2002), suggesting that predators from forest patches spill
421 over into cropped areas (Andrén, 1995). Predation rate by corvids decreased when the landscape
422 became more forest-dominated (forest density of 500 m²/ha) which agreed with previous studies
423 that showed high densities of corvids in agricultural-dominated landscapes (Andrén, 1992; Huhta et
424 al., 1996). In contrast, the probability of a nest being depredated by other predators, such as
425 mammals, was mainly influenced by the distance to hedgerows. Several studies reported that
426 predation activity of mammals can concentrate on linear habitat features such as hedgerows, as they
427 provide concealment and accessible travel routes through farmlands (Tryjanowski et al., 2002).
428 Hence, while hedgerows and forest patches provide heterogeneity to the farmland landscape
429 reducing predation pressure from corvids and providing benefits for the farmland biodiversity (Sirami
430 et al., 2019), they may also enhance predation by other predators having detrimental effects on
431 ground-nesting birds (Morris and Gilroy, 2008).

432 Although previous studies have reported that social status may affect the predation rate (Nilsen et
433 al., 2009), few studies have examined the link between landscape, abundance of predators, social
434 status, and predation rate. Our study found that the abundance of corvids with landscape
435 configuration varied with their social status. While corvid breeders were set in territories that could
436 be affected by landscape structure and food availability, floaters likely consisted of juvenile transient
437 flocks that foraged over greater distances than breeders, which usually concentrate on foraging

438 within smaller territories (Clayton and Emery, 2007). So, contrary to floaters, landscape structure
439 shapes the spatial distribution of corvid breeders, and so does their predation rate on ground nests.

440 **4.2. Effects of land use**

441 Our results revealed that the predation rate of ground nests in farmland landscapes is influenced by
442 the proportion of land use around the nest, suggesting a potential link between nest predation rates
443 and the availability of alternative food for mesopredators (Laidlaw et al., 2013). For instance,
444 agricultural intensification may lead to increased nest predation if it reduces the availability of
445 alternative food such as insects and seeds (Newton, 2004; Schmidt, 1999; Whittingham and Evans,
446 2004). Moreover, intensified agriculture may also result in a more uniform and dense vegetation
447 structure (Wilson et al., 2005), which reduces nesting opportunities, but also predator accessibility.
448 We found that the probability of a nest being depredated by corvids decreased when the landscape
449 was dominated by cereal crops (i.e., uniform and dense vegetation with low alternative food),
450 suggesting that corvids might actively avoid this kind of land use for searching for food (Saino, 1992).
451 Cereal crops are poor food resource patches with low densities of worms, insects, and seeds (Díaz
452 and Tellería, 1994) and their dense and tall vegetations makes them less accessible to corvids (Bravo
453 et al., 2022), which mainly forage by walking on the ground and relying on visual cues. Nest
454 predation by corvids and corvid abundance tended to decrease in landscapes dominated by
455 grasslands. Although grasslands may provide more food resources than spring crops (Møller, 1983),
456 they pose challenges for foraging due to dense vegetation, except when it is harvested. This result
457 might reflect that corvids preferentially forage in spring crops, leading to higher predator activity and
458 higher predation risk in these land uses. For ground-nesting birds, such as skylarks and lapwings,
459 which preferentially nest in spring crops due to their sparse vegetation and bare soil (Berg et al.,
460 2002; Chamberlain et al., 1999), this preference may create an ecological trap, increasing their
461 vulnerability in a homogeneous landscape dominated by spring crops.

462 Our results showed that the probability of predation by other predators was not affected by the
463 proportion of land use, suggesting that the effect of land use effect on the foraging strategies of
464 generalist predators may vary depending on the predator species (Chiavacci et al., 2018). For
465 example, in wet grassland landscapes, the rate of predation by foxes on wader nests might be
466 reduced through the management of land uses by patches providing a high abundance of small
467 mammals (Laidlaw et al., 2013). This is one of the few studies investigating the implications of land
468 use and availability of alternative food resources on predation risk and suggests this is an area of
469 conservation management that warrants critical attention.

470 The probability of corvid predation decreased throughout the breeding season in our study,
471 suggesting that the increased vegetation growth likely made it more challenging for visually oriented
472 predators, such as corvids, to locate nests. Conversely, our results suggested that other predators
473 relying on olfactory cues, such as mammals, might not be affected by vegetation growth. The
474 temporal variation in predation risk stresses the importance of considering dynamic processes when
475 investigating nest predation rates as it may be important for the evolution of life history traits (e. g.
476 the probability of laying replacement clutches may be affected by seasonal variation).

477

478 **4.3. Effects of roads and buildings**

479 Our findings indicate that the distance to human settlements did not have a significant impact on
480 artificial nest predation rate. The presence of corvids and other predators, such as red foxes and
481 stone martens, is likely to increase near human activities as they benefit from anthropogenic food
482 resources (Bateman and Fleming, 2012; Manton et al., 2019; Marzluff and Neatherlin, 2006).

483 Although their abundance may increase in urban environments, their predation rate may remain low,
484 giving rise to an urban predation paradox (Fischer et al., 2012). Likely, the availability of easily
485 accessible anthropogenic food resources might relax the predation rate close to human settlements
486 (Rodewald et al., 2011), thereby contributing to the observed lower predation rates.

487 Our results revealed that road density tended to decrease the predation rate and the abundance of
488 predators. Instead, we expected that road density increase corvid abundance and their nest
489 predation as 1) road densities affect ground-nesting birds like grey partridges (Harmange et al., 2019)
490 and little bustards (Cuscó et al., 2018) and 2) roads may be used by predators i) to move at night
491 (Kautz et al., 2021) and ii) during daylight for opportunistic vertebrate species that actively search for
492 carcasses from roadkills (Silva et al., 2019). Thus, the unexpected relationship between road density,
493 distance to human settlements, and the abundance of predators, as well as their predation rates,
494 highlights the importance of considering anthropogenic features, when investigating the spatial
495 dynamics of prey-predator interactions. The impact of roads and human settlements on predator-
496 prey relationships is complex and warrants further investigation.

497 **Perspectives for management**

498 Although conservation actions toward ground-nesting birds tend to focus on control and exclusion of
499 potential nest predators (Holt et al., 2008), much less attention has been paid to the management of
500 landscape attributes that can potentially mitigate the impact of predators (but see (Laidlaw et al.,
501 2021)). The LTSER 'Zone Atelier Plaine & Val de Sèvre' is undergoing a major change in land cover.
502 Cereal cover has increased by 20% in the last 20 years against permanent components of the
503 landscape (e.g., hedgerows) and grasslands (Bretagnolle et al., 2018). Our results showed that
504 landscape homogenisation may favour the predation rate of generalist mesopredators such as
505 corvids. A heterogeneous agricultural landscape that includes a mixture of crops associated with
506 patches of forests, hedgerows and grasslands offering alternative food to generalist predators might
507 reduce predation by corvids of ground-nesting birds. For instance, a forest density of 500m²/ha
508 reduced the likelihood of nest predation by corvids by 40% and the corvid predation rate was also
509 minimal with a hedgerow density of around 600 m²/ha or higher. Only 18% and 8% of our study area
510 comprised forest density beyond 500 m²/ha and hedgerow density of 600 m²/ha, respectively. Thus,

511 our study pleads for conservation actions of ground-nesting birds from landscape heterogeneity
512 management.

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519

520 **Authors' contributions**

521 Conceived and designed the experiments: CB VB OP MS. Performed the experiments: CB. Analysed
522 the data: CB OP. Wrote the paper: CB OP MS VB.

523

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Table 1. Landscape variables used to predict the probability of nest predation and corvid abundance in western France. For predation models, landscape variables were calculated around the location of each artificial nest, whereas, for models of corvid abundance, they were calculated around the point count location (see methods).

Independent variable (unit)	Description	Predation model			Corvid abundance model		
		Mean	SD	Range	Mean	SD	Range
<i>Landscape structure</i>							
Distance to hedgerow (m)	Distance from the artificial nest to the nearest hedgerow	42.56	21.15	[6.64 - 81.77]	-	-	-
Hedgerow density (m ² /ha)	Surface of tree lines forming a contiguous network across the farmed landscapes in a 300 m buffer	546.64	318.07	[42.69 - 1573.1]	536.44	289.1	[62.46 - 1265.64]
Forest density (m ² /ha)	Surface of forest patches in a 300 m buffer	78.44	130.70	[0 - 653.97]	63.15	81.22	[0 - 566.33]
<i>Alternative food variables</i>							

Cereal cover (%)	Proportion of area within 300 m buffer with cereal crops such as wheat and barley	36.06	20.14	[0 - 82.85]	38.87	21.20	[0-95.91]
Grassland cover (%)	Proportion of area within 300 m buffer with grassland crops such as meadows and alfalfa	19.86	17.60	[0 - 81.79]	17.26	17.31	[0-87.09]
Spring crop cover (%)	Proportion of area within 300 m buffer with spring crops such as sunflower and corn	24.73	18.96	[0 - 89.15]	24.38	19.32	[0-92.99]
Oilseed rape crop cover (%)	Proportion of area within 300 m buffer with oilseed rape crops	4.48	8.11	[0 - 31]	3.57	7.83	[0-51.64]
Other crops cover (%)	Proportion of area within 300 m buffer with other crops such as ryegrass, wax, peas, and lens	8.39	10.85	[0 - 51.36]	8.84	11.88	[0-87.09]
<i>Anthropogenic variables</i>							
Distance to human	Distance to the nearest human	306.72	197.35	[14.6-1309.3]	287.51	195.29	[17.95 - 1193.55]

settlements (m)

settlement such as a house,
farm, or village

Road density (m/ha)

Total length of paved roads in a
300 m buffer

47.38

14.36

[11.8-97.1]

46.18

14.53

[21.55 - 94.21]

Table 2. Effects of the distance to hedgerow, hedgerow density, forest density, and their quadratic terms, land use from a principal component analysis (PCA), and two-way interactions on the probability of a nest being depredated by corvid (left) or other predators (right) using GLMM (binomial, link = logit). PC1 and PC2 are the first two axes of PCA in land use variables (see methods). PC1 describes a gradient from landscapes dominated by grasslands to the ones dominated by cereal crops (Appendix 4 Table S5) and PC2 from grasslands to spring crops (Appendix 4 Table S5). The reference level for year is 2017 and *Others* for crop type (i.e., crop type in which nest was located). Asterisks indicated significant factors (i.e., 95% CI no overlapped the zero value).

Explanatory variables	Corvid predation model				Other predation model			
	Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper
			CI	CI			CI	CI
(Intercept)	-1.19	0.75	-2.66	0.28	-6.03	1.17	-8.32	-3.75
Distance to hedgerow	0.65	0.21	0.25	1.06*	-0.22	0.50	-1.20	0.75
Distance to hedgerow ²	-0.12	0.10	-0.31	0.08	-0.57	0.22	-1.01	-0.13*
Hedgerow density	-0.32	0.15	-0.61	-0.02*	0.06	0.24	-0.40	0.53
Hedgerow density ²	0.22	0.13	-0.04	0.47	-0.16	0.23	-0.61	0.30
Forest density	-0.10	0.31	-0.70	0.50	-0.65	0.50	-1.62	0.32
Forest density ²	-0.21	0.23	-0.67	0.24	-0.08	0.41	-0.88	0.72
PC1	-0.45	0.19	-0.82	-0.09*	-0.21	0.39	-0.97	0.55
PC2	-0.02	0.16	-0.32	0.29	0.31	0.32	-0.31	0.93
Crop type (Cereals)	-1.34	0.27	-1.87	-0.82*	0.04	0.46	-0.87	0.95
Crop type (Grasslands)	0.97	0.27	0.44	1.49*	0.63	0.56	-0.46	1.72
Crop type (Spring crops)	1.79	0.36	1.09	2.49*	-0.46	0.80	-2.03	1.11
Julian day	-0.01	0.00	-0.02	0.00*	0.01	0.01	-0.01	0.02
Year (2018)	-0.59	0.22	-1.01	-0.16*	1.14	0.43	0.29	1.98*

Year (2019)	-0.12	0.27	-0.64	0.40	1.67	0.48	0.73	2.60*
Distance to hedgerow × Crop type (Cereals)	-0.73	0.27	-1.26	-0.20*	0.28	0.54	-0.78	1.34
Distance to hedgerow × Crop type (Grasslands)	-0.29	0.26	-0.79	0.22	0.19	0.65	-1.08	1.47
Distance to hedgerow × Crop type (Spring crops)	-0.75	0.28	-1.31	-0.20*	1.30	0.78	-0.22	2.83
PC1 × Crop type (Cereals)	0.72	0.24	0.26	1.19*	-0.04	0.41	-0.84	0.76
PC1 × Crop type (Grasslands)	0.40	0.23	-0.05	0.85	0.39	0.47	-0.53	1.32
PC1 × Crop type (Spring crops)	0.30	0.26	-0.22	0.82	0.14	0.58	-0.99	1.27
PC2 × Crop type (Cereals)	0.15	0.23	-0.30	0.60	-0.16	0.37	-0.89	0.57
PC2 × Crop type (Grasslands)	-0.05	0.20	-0.45	0.35	-0.01	0.47	-0.92	0.90
PC2 × Crop type (Spring crops)	0.32	0.23	-0.13	0.76	-0.18	0.52	-1.20	0.84
Hedgerow density × Forest density	-0.09	0.22	-0.51	0.33	0.88	0.41	0.08	1.68*
Distance to hedgerow × Hedgerow density	0.19	0.11	-0.01	0.40	-0.46	0.27	-1.00	0.07
Distance to hedgerow × Forest density	-0.04	0.16	-0.35	0.27	0.93	0.39	0.17	1.68*
PC1 × Hedgerow density	0.12	0.11	-0.10	0.33	-0.29	0.19	-0.67	0.09
PC1 × Forest density	0.13	0.16	-0.19	0.45	-0.30	0.30	-0.89	0.29
PC1 × Distance to hedgerow	0.15	0.09	-0.03	0.34	0.12	0.19	-0.25	0.49
PC2 × Hedgerow density	0.09	0.09	-0.09	0.27	0.16	0.19	-0.21	0.52
PC2 × Forest density	-0.09	0.16	-0.40	0.22	-0.08	0.29	-0.64	0.48
PC2 × Distance to hedgerow	0.04	0.09	-0.13	0.21	0.10	0.19	-0.27	0.47

Table 3. Effects of the distance to hedgerow, hedgerow density, forest density, their quadratic terms, land use from a principal component analysis (PCA), and two-way interactions on the abundance of corvid breeders (A) or floaters (B) using GLM (Poisson error distribution, link = logit). PC1 and PC2 are the first two axes of a principal component analysis on land use variables (see methods). PC1 describes a gradient from landscapes dominated by grasslands to the ones dominated by cereal crops (Appendix 4 Table S5) and PC2 from grasslands to spring crops (Appendix 4 Table S5).

Response variable	Explanatory variables	Estimate	SE	Lower CI	Upper CI
A. Corvid breeder		1.55	0.09	1.37	1.72
	Hedgerow density	-0.03	0.06	-0.15	0.09
	Hedgerow density²	0.14	0.06	0.02	0.26
	Forest density	0.29	0.13	0.04	0.54
	Forest density²	-0.42	0.12	-0.65	-0.19
	PC1	0.03	0.05	-0.07	0.13
	PC2	0.06	0.05	-0.05	0.16
	Hedgerow density × Forest density	-0.06	0.12	-0.30	0.17
	PC1 × Hedgerow density	0.05	0.05	-0.05	0.14
	PC1 × Forest density	-0.01	0.1	-0.20	0.18
	PC2 × Hedgerow density	0.08	0.04	0.00	0.16
	PC2 × Forest density	-0.13	0.1	-0.32	0.06
B. Corvid floater		1.71	0.07	1.56	1.85
	Hedgerow density	-0.41	0.05	-0.50	-0.32
	Hedgerow density²	0.23	0.05	0.14	0.32
	Forest density	-0.22	0.1	-0.42	-0.02
	Forest density²	0.33	0.09	0.15	0.50

PC1	-0.24	0.04	-0.31	-0.16
PC2	0.19	0.04	0.11	0.27
Hedgerow density × Forest density	-0.1	0.08	-0.26	0.05
PC1 × Hedgerow density	0.15	0.04	0.08	0.23
PC1 × Forest density	-0.09	0.07	-0.22	0.05
PC2 × Hedgerow density	0.02	0.03	-0.04	0.08
PC2 × Forest density	0.33	0.07	0.19	0.47

Fig. 1. A) Location of the sampling points in the study area within the Long-Term Social-Ecological Research (LTSER) site 'Zone Atelier Plaine & Val de Sèvre' (France). Note the sampling points were stratified according to hedgerow density. B) Image of a sampling point showing the location of the artificial nests (n =2576) and the location of the point count to estimate the corvid abundance. Note that transects were set parallel to the hedgerow at 10 m, 30 m, 50 m, and 70 m (one distance per sampling point).

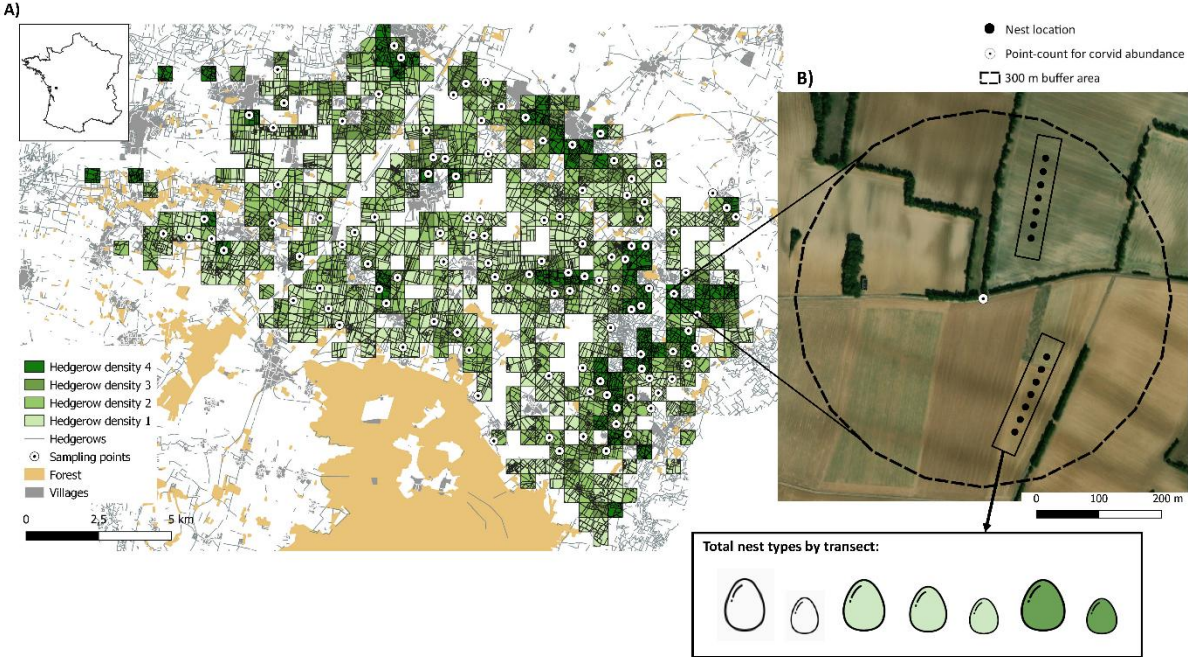


Fig. 2. Quadratic effect of the distance to hedgerow on the probability of a nest being depredated by corvids (A) and other predators (B) splitting by the crop type in which nest is located (spring crops, grasslands, cereal crops, and others). Full line is the predicted values (with \pm 95% CI) extracted from GLMM detailed in Table 2.

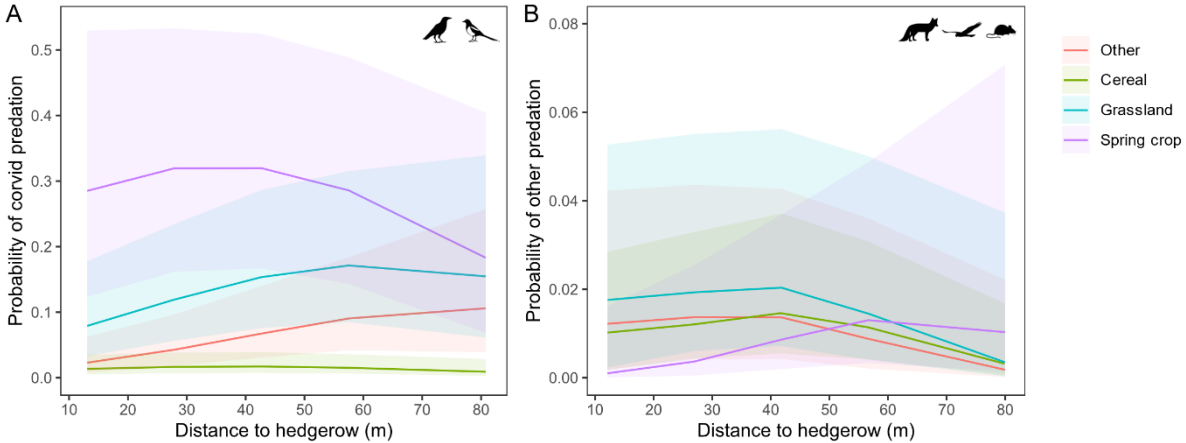


Fig. 3. Effects of hedgerow and forest densities on the probability of a nest being depredated by corvids. Predicted values (i.e., surface) are extracted from a GLMM detailed in Table 2. The grey and bottom points represent the distribution of observed values.

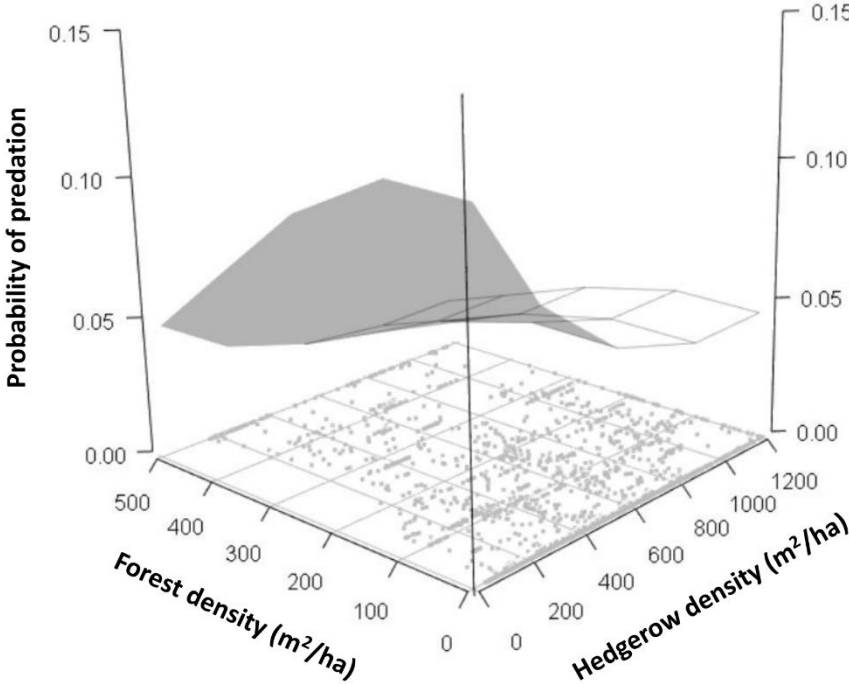


Fig. 4. Effect of land use as a gradient from grasslands and spring crops to cereals (indicated by the first axis of a principal component, PC1) on the probability of a nest being depredated by corvids splitting by the crop type in which nest was located (spring crop, grassland, cereal and other). Predicted values $\pm 95\%$ CI are extracted from a GLMM (Table 2). The first axis of the principal component analysis on land use proportions is detailed in Appendix 4.

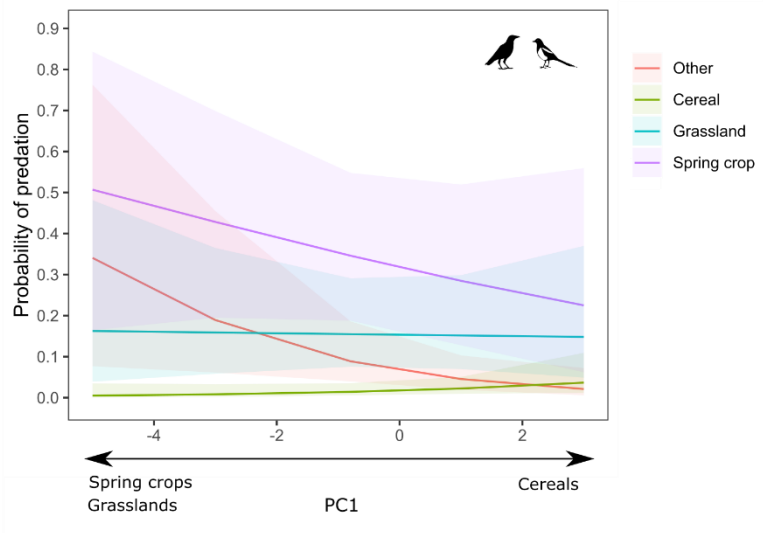
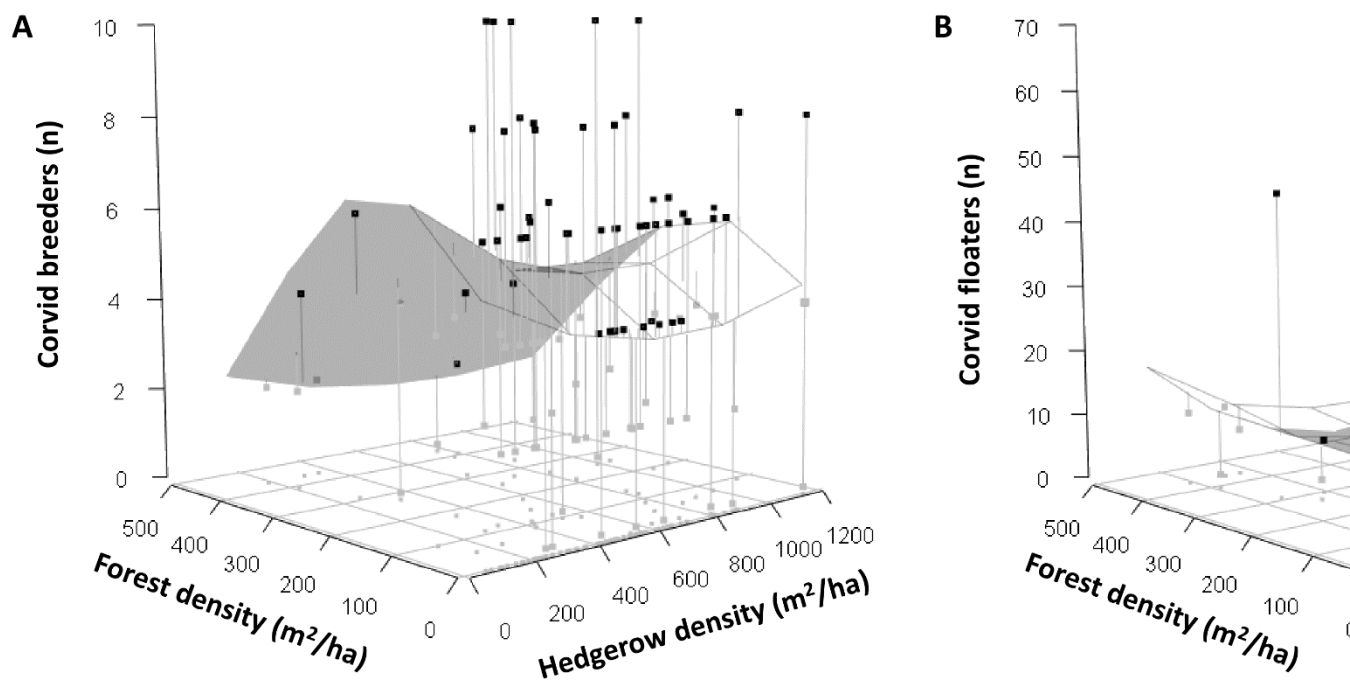


Fig. 5. Effects of the hedgerow and forest densities on the abundance of corvid breeders (A) and floaters (B). Predicted values (surface) are extracted from a GLM on breeders and floaters (detailed in Table 3A and B, respectively). Black and grey dots are the observed values that are respectively higher and lower than the predicted abundances of corvids. The bottom grey dots represent the distribution of observed values.



SUPPLEMENTARY MATERIAL: Hedgerows interact with forests to shape the abundance of mesopredators and their predation rate on eggs in farmland landscapes

Includes:

Appendix 1: No linear DSR

Fig. S1. Estimated daily survival rate of artificial nests in relation to the monitoring day and splitting by year.

Appendix 2

Table S2. Distribution of egg color and egg size artificial nests in relation to year. Notice that in 2017 the exposure time was 7 days and in 2018 and 2019 it was 15 days.

Table S3. Summary of corvid abundance (n) by sampling point (n=112). The mean \pm SD and percentage of sampling points with the presence of corvids between brackets is shown. Data is splitting by year and total corresponds with the sum of individuals of the three years.

Appendix 3: Selection of buffer size

Table S4. Results of the model selection of the effect of buffer size on corvid predation and on corvid abundance.

Fig. S2. Comparison of model support for the effect of buffer size on the probability of corvid predation (dashed line) and on corvid abundance (solid line). The estimated scale of effect is the buffer size with the smallest AIC. Model selection rank is presented in Table S3.

Appendix 4: Quantification of alternative foods

Table S5. Loadings of land use proportions on the first two axes extracted by a PCA for predation (A) and for corvid abundance (B) model, after a varimax normalised rotation, and the proportion of variance accounted for by each axis.

Fig. S3. Loadings of land use proportions on the first two axes extracted by a PCA for predation (A) and for corvid abundance (B) model, after a varimax normalised rotation, and the proportion of variance accounted for by each axis.

Appendix 5: Temporal effects

Fig. S4. Probability of corvid predation (left) and other predation (right) in relation to hedgerow density and forest density splitting by year.

Fig. S5. Probability of corvid breeder abundance (left) and floater abundance (right) in relation to hedgerow density and forest density splitting by year.

Fig. S6. Probability of corvid predation (left) and other predation (right) in relation to julian day.

Appendix 6: Spatial autocorrelation

Fig. S7. Moran's I correlogram of the residuals of the corvid predation (left) and other predation (right). The Moran's I (spatial autocorrelation index) is calculated for different distance classes: 0-1000m, 1000-2000m, ..., 19000-20000m. Red points show distance classes at which there is spatial autocorrelation in the model's residuals.

Fig. S8. Moran's I correlogram of the residuals of the corvid breeder abundance (left) and corvid floater abundance (right). The Moran's I (spatial autocorrelation index) is calculated for different distance classes: 0-1000m, 1000-2000m, ..., 19000-20000m. Red points show distance classes at which there is spatial autocorrelation in the model's residuals.

Appendix 7: Corvid abundance in relation to food alternative and anthropogenic variables

Fig. S9. Effect of land use as (A) a gradient from grasslands and spring crops to cereals (indicated by the first axis of a principal component, PC1) and as (B) a gradient from grasslands to spring crops (indicated by the second axis PC2) on the corvid abundance ($\pm 95\%$ CI). PC1 describes a gradient of points dominated by cereal crops (Appendix 4). PC2 describes a gradient of points dominated by spring crops (Appendix 4). Corvid breeder (red) and corvid floater (blue).

Fig. S10. Effects of (A) hedgerow density at different levels of cereal crop proportion (PC1), and (B) forest density at different levels of spring crop proportion (PC2) on corvid floater abundance ($\pm 95\%$ CI). PC1 describes a gradient of points dominated by cereal crops (Appendix 4). PC2 describes a gradient of points dominated by spring crops (Appendix 4).

Fig. S11. Effects of hedgerow density (A) and forest density (B) at different levels of road density on corvid floater abundance ($\pm 95\%$ CI).

Appendix 8: Relationship between corvid abundance and predation rates

Table S6. Effects of the distance to hedgerow, hedgerow density, forest density, and their quadratic terms, land use from a principal component analysis (PCA), and two-way interactions on the probability of a nest being depredated by corvid (i) without including corvid abundance variable; (ii) including breeder abundance variable, and (iii) including floater abundance variable using GLMM (binomial, link = logit). PC1 and PC2 are the first two axes of PCA in land use variables (see methods). PC1 describes a gradient from landscapes dominated by grasslands to the ones dominated by cereal crops (Appendix 4 Table S5) and PC2 from grasslands to spring crops (Appendix 4 Table S5). The reference level for year is *2017* and *Others* for crop type (i.e., crop type in which nest was located). Bold indicated significant factors (i.e., 95% CI no overlapped the zero value). Effect size was computed with the Odds ratio.

Appendix 1: No linear DSR

We calculated the daily survival rate of nests (DSR), that is, the probability of survival of a nest for one day within a given time interval, and used “Nest Survival” function in MARK program using the RMark package (Cooch and White 2012), a procedure that allowed considering that DSR is not constant with time. The exposure time of eggs to predation was 7 or 15, depending on the year. To control for temporal structure in our dataset, we included day of monitoring with its quadratic term to consider that DSR might not constantly vary with time. The effect of Year was also included in the model. A temporal quadratic variation in DSR was apparent. DSR increased significantly by 2-9% on the monitoring day (Fig. S1). Given that DSR followed a quadratic pattern and therefore, DSR was not constant along the monitoring, and because monitoring days differed between years, we used the predation rate at day 3 (obtained all three years) as a standardized measure of predation rate.

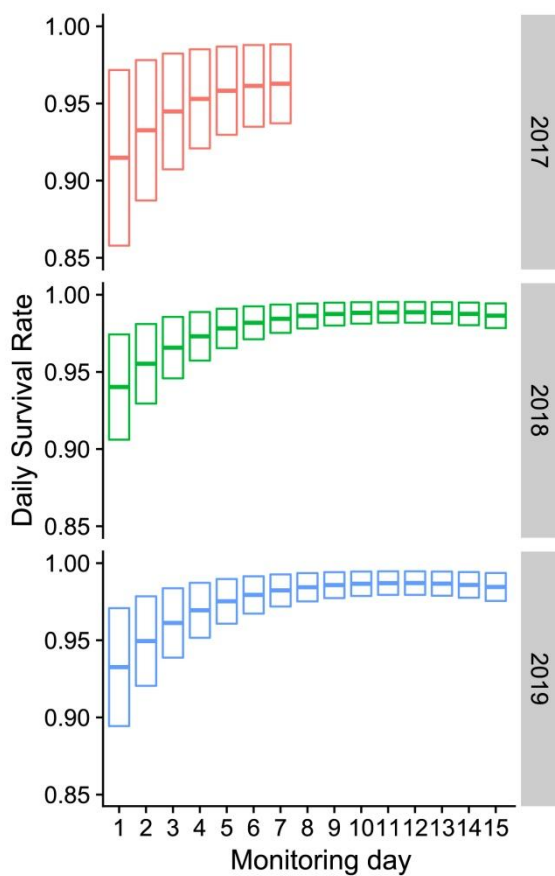


Fig. S1. Estimated daily survival rate of artificial nests in relation to the monitoring day and splitting by year.

Appendix 2

Table S2. Distribution of egg color and egg size artificial nests in relation to year. Notice that in 2017 the exposure time was 7 days and in 2018 and 2019 it was 15 days.

Egg color	Egg size	2017	2018	2019	Total
White	Large	224	226	112	562
	Small	224	225	111	560
Light green	Large	223			223
	Small	224			224
	Medium		224	113	337
Dark green	Large		225	111	336
	Small		224	110	334
Total		895	1124	557	2576

Table S3. Summary of corvid abundance (n) by sampling point (n=112). The mean \pm SD and percentage of sampling points with the presence of corvids between brackets is shown. Data is splitting by year and total corresponds with the sum of individuals of the three years.

	Total corvid	Corvid breeder	Corvid floater
2017	3.37 \pm 4.91 (89.29)	2.33 \pm 0.82 (54.46)	2.94 \pm 5.3 (69.64)
2018	5.21 \pm 8.44 (92.86)	2.49 \pm 0.86 (76.79)	4.87 \pm 9.7 (67.86)
2019	3.94 \pm 3.99 (91.07)	2.43 \pm 0.82 (41.96)	3.59 \pm 4.14 (81.25)
Total	12.46 \pm 11.27 (100)	4.7 \pm 2.23 (89.29)	8.34 \pm 10.62 (99.11)

Appendix 3: Selection of buffer size

We selected a 300 m buffer from each artificial nest and from each point count to calculate the landscape variables. This buffer size showed the best-fitted model compared with other buffer sizes (i.e., 100, 200, 300, 400 and 500 m) for both predation and corvid abundance (Table S4, Fig. S2).

Table S4. Results of the model selection of the effect of buffer size on corvid predation and on corvid abundance.

Model	Buffer size	K	AICc	$\Delta AICc$	AICcw
Corvid predation	300	11	2254.25	0	0.85
	400	11	2258.48	4.23	0.1
	500	11	2260.34	6.09	0.04
	200	11	2263.06	8.81	0.01
	100	11	2271.35	17.1	0
Corvid abundance	300	6	546.15	0.00	0.57
	200	6	548.43	2.27	0.18
	100	6	549.62	3.47	0.10
	400	6	549.78	3.62	0.09
	500	6	550.91	4.76	0.05

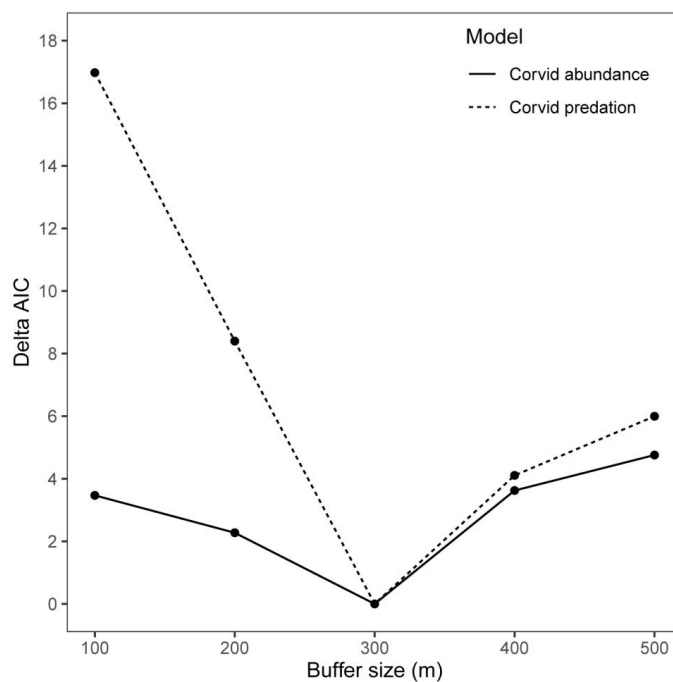


Fig. S2. Comparison of model support for the effect of buffer size on the probability of corvid predation (dashed line) and on corvid abundance (solid line). The estimated scale of effect is the buffer size with the smallest AIC. Model selection rank is presented in Table S4.

Appendix 4: Quantification of alternative foods

As proportions of land use were autocorrelated, a Principal Component Analysis (PCA) of the proportions of land use was used to derive summarizing descriptors of characteristic land uses.

For nest location, the first two axes of PCA accounted for 58.7% of the variation in the data. The first axis, which explained 31.2% of the variance, described a gradient of points from those dominated by grasslands and spring crops to those dominated by cereal crops (eigenvectors: Cereal = 0.75, Table S5). The second axis, which explained 27.5% of the variance, distinguished a gradient of points from those dominated by grasslands to those dominated by spring crops (eigenvectors: grasslands = -0.44; spring crops = 0.72, Table S5).

For corvid abundance, the first two axes of this PCA accounted for 56.3% of the variation in the data. The first axis, which explained 31% of the variance, described a gradient of points from those dominated by grasslands and spring crops to those dominated by cereal crops (eigenvectors: Cereal = 0.65, Table S5). The second axis, which explained 25.3% of the variance, distinguished a gradient of points from those dominated by grasslands to those dominated by spring crops (eigenvectors: grasslands = -0.72; spring crops = 0.64, Table S5).

In both predation and corvid abundance, the first axis revealed a major gradient largely reflecting accessibility and food availability. Grasslands and spring crops provide easy access and unhindered ground locomotion as well as tend to have a higher abundance of insects and seeds, whereas cereal crops are characterised by tall and dense vegetation, generally poor in food availability. Food availability was also reflected in a secondary gradient contrasting spring crops and grasslands (PC2), where grasslands are richer in food resources than spring crops. Therefore, PC1 reflects a gradient potentially decreasing accessibility and food availability, and PC2 reflects a gradient of potentially decreasing food availability in easily accessible land uses.

Table S5. Loadings of land use proportions on the first two axes extracted by a PCA for predation (A) and for corvid abundance (B) model, after a varimax normalised rotation, and the proportion of variance accounted for by each axis.

	Predation model		Abundance model	
	PC1	PC2	PC1	PC2
Cereals	0.75	-0.09	0.65	-0.03
Grasslands	-0.49	-0.44	-0.42	-0.72
Spring crops	-0.35	0.72	-0.52	0.64
Oilseed rape crops	0.06	-0.31	0.19	-0.12
Other	-0.27	-0.44	0.3	0.24
Variance explained	31.2%	27.5%	31%	25.3%

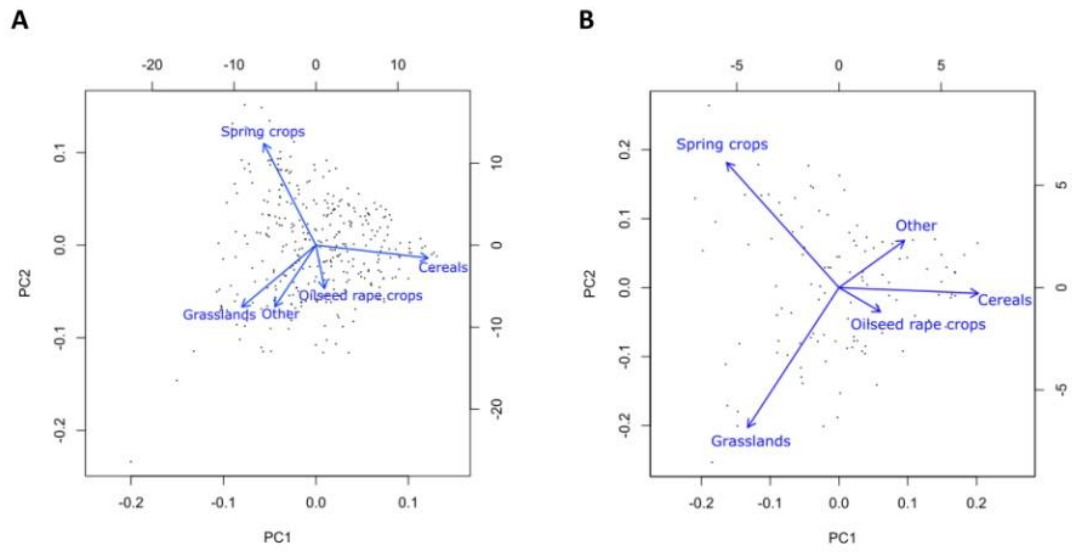


Fig. S3. Loadings of land use proportions on the first two axes extracted by a PCA for predation (A) and for corvid abundance (B) model, after a varimax normalised rotation, and the proportion of variance accounted for by each axis.

Appendix 5: Temporal effects

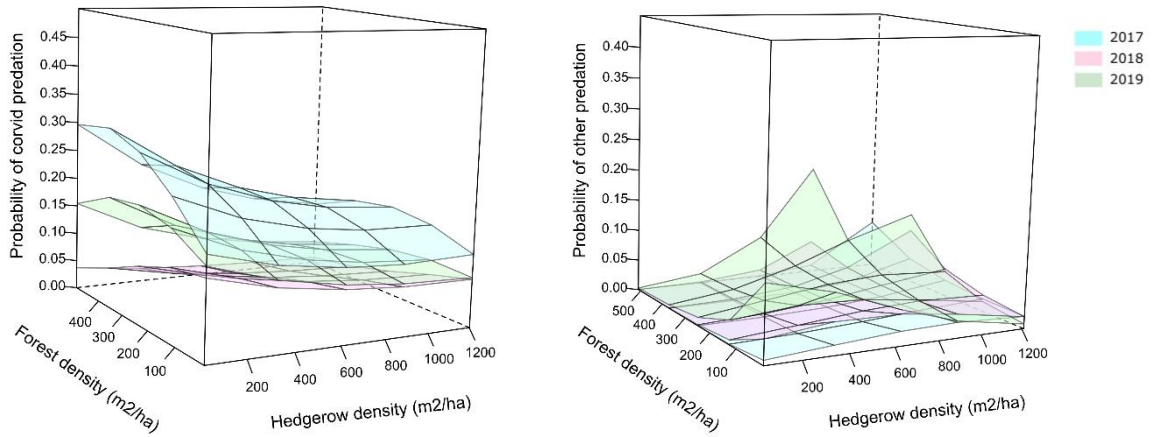


Fig. S4. Probability of corvid predation (left) and other predation (right) in relation to hedgerow density and forest density splitting by year.

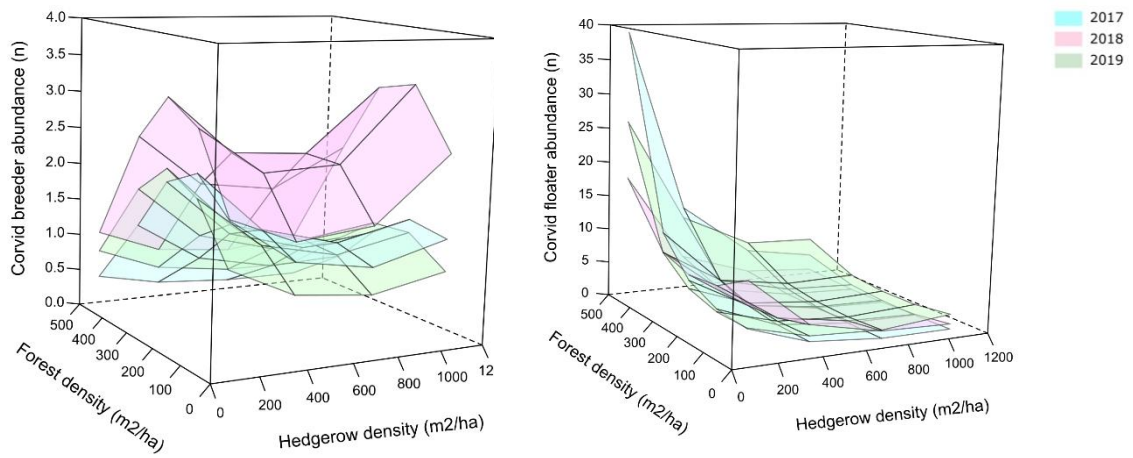


Fig. S5. Probability of corvid breeder abundance (left) and floater abundance (right) in relation to hedgerow density and forest density splitting by year.

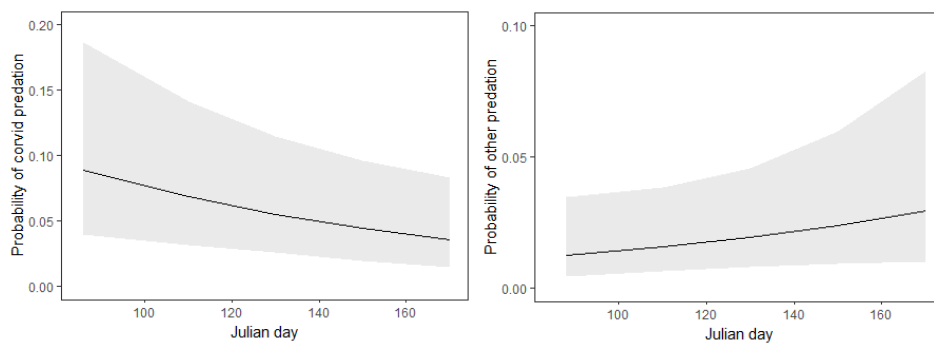


Fig. S6. Probability of corvid predation (left) and other predation (right) in relation to Julian day.

Appendix 6: Spatial autocorrelation

We assessed spatial autocorrelation in the residual models through a Moran's I correlogram.

We verified the lack of spatial autocorrelation through a Moran's I correlogram of the model residuals of corvid predation and other predation (Fig. S7).

We verified the lack of spatial autocorrelation through a Moran's I correlogram of the model residuals of breeder abundance and floater abundance (Fig. S8).

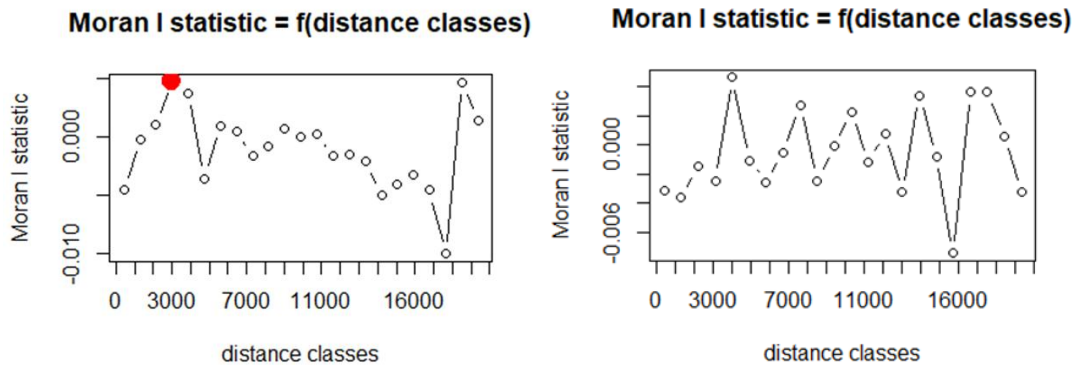


Fig. S7. Moran's I correlogram of the residuals of the corvid predation (left) and other predation (right). The Moran's I (spatial autocorrelation index) is calculated for different distance classes: 0-1000m, 1000-2000m, ..., 19000-20000m. Red points show distance classes at which there is spatial autocorrelation in the model's residuals.

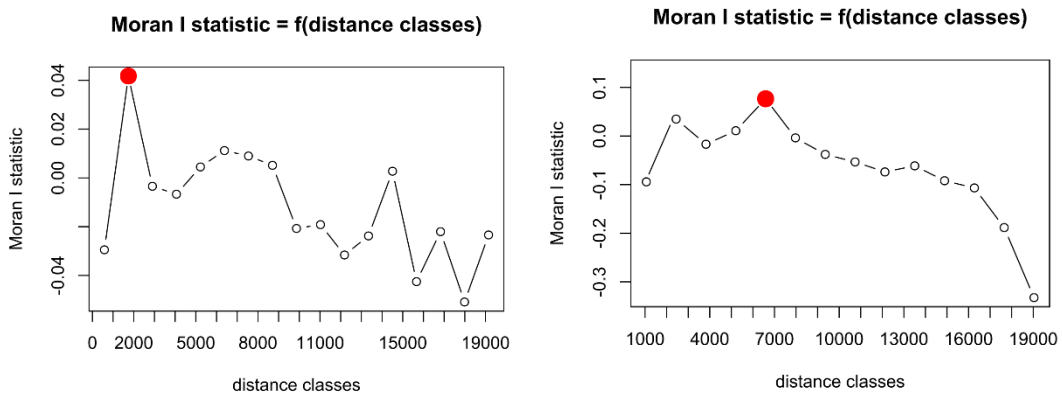


Fig. S8. Moran's I correlogram of the residuals of the corvid breeder abundance (left) and corvid floater abundance (right). The Moran's I (spatial autocorrelation index) is calculated for different distance classes: 0-1000m, 1000-2000m, ..., 19000-20000m. Red points show distance classes at which there is spatial autocorrelation in the model's residuals.

Appendix 7: Corvid abundance in relation to food alternative and anthropogenic variables

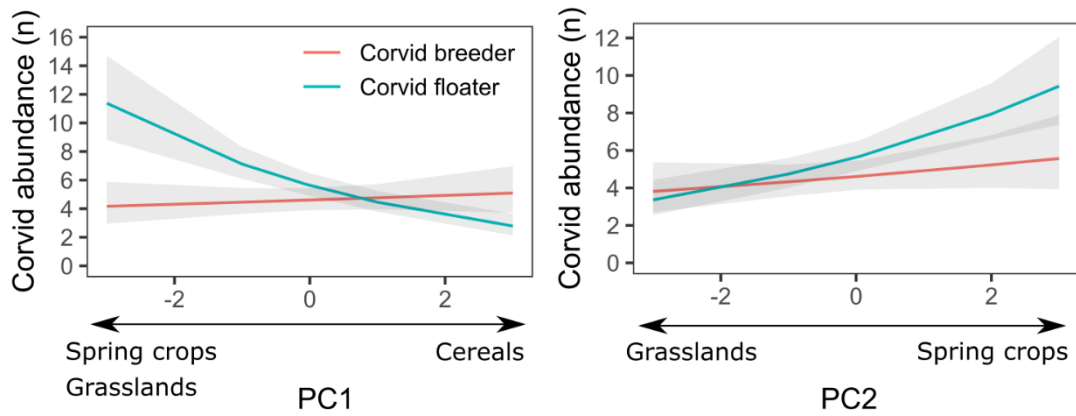


Fig. S9. Effect of land use as (A) a gradient from grasslands and spring crops to cereals (indicated by the first axis of a principal component, PC1) and as (B) a gradient from grasslands to spring crops (indicated by the second axis PC2) on the corvid abundance ($\pm 95\%$ CI). PC1 describes a gradient of points dominated by cereal crops (Appendix 4). PC2 describes a gradient of points dominated by spring crops (Appendix 4). Corvid breeder (red) and corvid floater (blue).

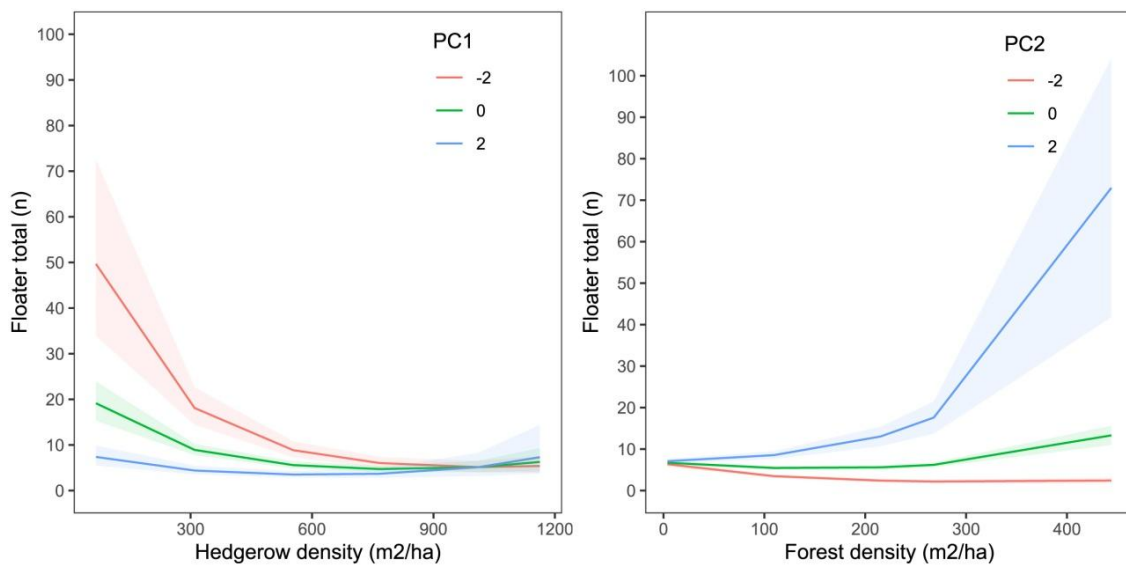


Fig. S10. Effects of (A) hedgerow density at different levels of cereal crop proportion (PC1), and (B) forest density at different levels of spring crop proportion (PC2) on corvid floater abundance ($\pm 95\%$ CI). PC1 describes a gradient of points dominated by cereal crops (Appendix 4). PC2 describes a gradient of points dominated by spring crops (Appendix 4).

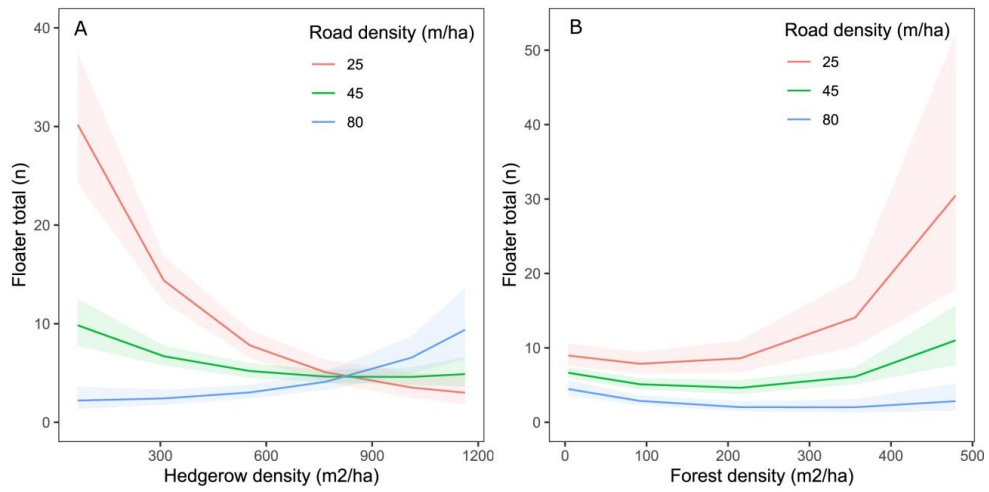


Fig. S11. Effects of hedgerow density (A) and forest density (B) at different levels of road density on corvid floater abundance ($\pm 95\%$ CI).

Appendix 8: Relationship between corvid abundance and predation rates

Table S6. Effects of the distance to hedgerow, hedgerow density, forest density, and their quadratic terms, land use from a principal component analysis (PCA), and two-way interactions on the probability of a nest being depredated by corvid (i) without including corvid abundance variable; (ii) including breeder abundance variable, and (iii) including floater abundance variable using GLMM (binomial, link = logit). PC1 and PC2 are the first two axes of PCA in land use variables (see methods). PC1 describes a gradient from landscapes dominated by grasslands to the ones dominated by cereal crops (Appendix 4 Table S5) and PC2 from grasslands to spring crops (Appendix 4 Table S5). The reference level for year is *2017* and *Others* for crop type (i.e., crop type in which nest was located). Bold indicated significant factors with 95% CI that did not overlap the zero value. Effect size was computed with the Odds ratio.

Explanatory variables	i) Model without corvid abundance (AIC=1621.34)						ii) Breeder model (AIC=1603.51)						iii) Floater model (AIC=1623.34)					
	Estimate	SE	Lower CI	Upper CI	Odds ratio	Odds CI 95%	Estimate	SE	Lower CI	Upper CI	Odds ratio	Odds CI 95%	Estimate	SE	Lower CI	Upper CI	Odds ratio	Odds CI 95%
(Intercept)	-1.10	0.75	-2.57	0.37	0.08	[0.03,0.19]	-2.02	0.77	-3.54	-0.51	0.08	[0.03,0.19]	-1.09	0.76	-2.57	0.39	0.08	[0.03,0.19]
Distance to hedgerow	0.59	0.20	0.19	0.99	1.79	[1.21,2.67]	0.65	0.20	0.25	1.04	1.9	[1.29,2.82]	0.59	0.20	0.19	0.99	1.8	[1.21,2.67]
Distance to hedgerow ²	-0.10	0.11	-0.31	0.12	0.91	[0.73,1.12]	-0.12	0.11	-0.33	0.09	0.89	[0.72,1.09]	-0.10	0.11	-0.31	0.11	0.91	[0.73,1.12]
Hedgerow density	-0.33	0.15	-0.63	-0.03	0.72	[0.55,0.96]	-0.26	0.14	-0.55	0.02	0.77	[0.59,1.00]	-0.33	0.16	-0.64	-0.02	0.73	[0.54,0.97]
Hedgerow density ²	0.20	0.13	-0.06	0.45	1.2	[0.95,1.50]	0.20	0.12	-0.05	0.44	1.19	[0.96,1.48]	0.20	0.13	-0.06	0.45	1.2	[0.95,1.51]
Forest density	-0.11	0.31	-0.71	0.49	0.95	[0.60,1.49]	-0.22	0.29	-0.79	0.36	0.86	[0.56,1.33]	-0.10	0.31	-0.70	0.51	0.95	[0.60,1.49]
Forest density ²	-0.19	0.23	-0.65	0.27	0.91	[0.73,1.13]	-0.02	0.23	-0.46	0.43	0.99	[0.80,1.23]	-0.20	0.23	-0.66	0.26	0.91	[0.73,1.13]
PC1	-0.40	0.19	-0.76	-0.03	0.61	[0.39,0.95]	-0.37	0.19	-0.73	-0.01	0.63	[0.41,0.98]	-0.40	0.19	-0.77	-0.03	0.61	[0.39,0.95]
PC2	0.00	0.16	-0.31	0.31	1	[0.70,1.43]	-0.02	0.15	-0.32	0.29	0.98	[0.69,1.39]	0.00	0.16	-0.31	0.31	1	[0.70,1.43]
Crop type (Cereals)	-1.40	0.27	-1.93	-0.86	0.24	[0.14,0.41]	-1.43	0.27	-1.96	-0.90	0.23	[0.13,0.39]	-1.39	0.27	-1.92	-0.86	0.24	[0.14,0.41]
Crop type (Grasslands)	0.94	0.27	0.42	1.47	2.54	[1.50,4.28]	0.86	0.26	0.34	1.38	2.34	[1.39,3.92]	0.94	0.27	0.42	1.47	2.54	[1.50,4.29]
Crop type (Spring crops)	1.74	0.36	1.04	2.44	5.57	[2.77,11.22]	1.71	0.35	1.02	2.41	5.44	[2.73,10.86]	1.74	0.36	1.03	2.44	5.54	[2.74,11.17]
Corvid abundance							0.23	0.05	0.13	0.32	1.78	[1.39,2.28]	0.00	0.01	-0.02	0.03	1	[0.77,1.31]
Julian day	-0.01	0.00	-0.02	0.00	0.77	[0.63,0.95]	-0.01	0.00	-0.02	0.00	0.77	[0.62,0.94]	-0.01	0.00	-0.02	0.00	0.77	[0.63,0.95]
Year (2018)	-0.54	0.22	-0.97	-0.11	0.58	[0.38,0.89]	-0.55	0.22	-0.98	-0.12	0.58	[0.38,0.88]	-0.54	0.22	-0.97	-0.12	0.58	[0.38,0.89]
Year (2019)	-0.11	0.27	-0.64	0.41	0.89	[0.53,1.50]	-0.16	0.27	-0.68	0.36	0.85	[0.51,1.44]	-0.12	0.27	-0.64	0.41	0.89	[0.53,1.50]
Distance to hedgerow × Crop type (Cereals)	-0.87	0.28	-1.41	-0.32	0.42	[0.24,0.72]	-0.92	0.28	-1.47	-0.38	0.4	[0.23,0.68]	-0.86	0.28	-1.41	-0.32	0.42	[0.24,0.72]
Distance to hedgerow × Crop type (Grasslands)	-0.10	0.26	-0.61	0.40	0.9	[0.54,1.49]	-0.13	0.25	-0.63	0.37	0.88	[0.53,1.44]	-0.10	0.26	-0.60	0.41	0.9	[0.54,1.49]
Distance to hedgerow × Crop type (Spring crops)	-0.80	0.28	-1.35	-0.25	0.45	[0.26,0.78]	-0.82	0.28	-1.36	-0.27	0.44	[0.25,0.76]	-0.80	0.28	-1.35	-0.24	0.45	[0.26,0.78]

PC1 × Crop type (Cereals)	0.69	0.24	0.22	1.17	2.33	[1.31,4.12]	0.74	0.24	0.26	1.21	2.44	[1.37,4.34]	0.70	0.24	0.23	1.17	2.33	[1.31,4.13]
PC1 × Crop type (Grasslands)	0.32	0.23	-0.13	0.77	1.47	[0.86,2.54]	0.28	0.23	-0.16	0.73	1.41	[0.82,2.41]	0.32	0.23	-0.13	0.77	1.47	[0.85,2.54]
PC1 × Crop type (Spring crops)	0.21	0.26	-0.30	0.73	1.3	[0.70,2.44]	0.14	0.26	-0.37	0.66	1.19	[0.64,2.21]	0.22	0.26	-0.30	0.74	1.3	[0.69,2.42]
PC2 × Crop type (Cereals)	0.14	0.23	-0.31	0.59	1.18	[0.70,1.99]	0.21	0.23	-0.25	0.66	1.28	[0.75,2.17]	0.14	0.23	-0.31	0.59	1.18	[0.70,2.00]
PC2 × Crop type (Grasslands)	-0.14	0.20	-0.53	0.26	0.86	[0.54,1.36]	-0.12	0.20	-0.51	0.27	0.87	[0.55,1.38]	-0.13	0.20	-0.53	0.26	0.86	[0.54,1.36]
PC2 × Crop type (Spring crops)	0.28	0.23	-0.16	0.73	1.4	[0.83,2.36]	0.29	0.22	-0.15	0.72	1.4	[0.84,2.33]	0.29	0.23	-0.16	0.74	1.41	[0.83,2.37]
Hedgerow density × Forest density	-0.05	0.22	-0.48	0.38	0.96	[0.73,1.28]	-0.11	0.21	-0.52	0.31	0.93	[0.71,1.22]	-0.05	0.22	-0.48	0.38	0.97	[0.73,1.28]
Distance to hedgerow × Hedgerow density	0.13	0.10	-0.07	0.34	1.13	[0.93,1.38]	0.13	0.10	-0.07	0.33	1.13	[0.93,1.37]	0.13	0.10	-0.07	0.34	1.14	[0.94,1.38]
Distance to hedgerow × Forest density	0.06	0.16	-0.24	0.37	1.04	[0.84,1.29]	0.04	0.16	-0.27	0.34	1.02	[0.83,1.26]	0.06	0.16	-0.25	0.37	1.05	[0.84,1.29]
PC1 × Hedgerow density	0.07	0.11	-0.15	0.28	1.08	[0.84,1.38]	0.08	0.11	-0.13	0.28	1.09	[0.86,1.38]	0.07	0.11	-0.15	0.28	1.08	[0.84,1.38]
PC1 × Forest density	0.11	0.17	-0.22	0.44	1.09	[0.83,1.44]	0.09	0.16	-0.24	0.41	1.07	[0.82,1.40]	0.10	0.17	-0.22	0.43	1.09	[0.83,1.44]
PC1 × Distance to hedgerow	0.01	0.09	-0.18	0.19	1.01	[0.81,1.26]	0.01	0.09	-0.18	0.19	1.01	[0.81,1.26]	0.01	0.09	-0.18	0.19	1.01	[0.80,1.26]
PC2 × Hedgerow density	0.10	0.09	-0.08	0.28	1.12	[0.92,1.37]	0.04	0.09	-0.14	0.21	1.04	[0.86,1.26]	0.10	0.09	-0.08	0.28	1.12	[0.92,1.36]
PC2 × Forest density	-0.08	0.16	-0.39	0.23	0.93	[0.73,1.20]	-0.04	0.15	-0.34	0.26	0.97	[0.76,1.23]	-0.09	0.16	-0.40	0.23	0.93	[0.73,1.20]
PC2 × Distance to hedgerow	0.06	0.08	-0.10	0.23	1.08	[0.89,1.30]	0.04	0.08	-0.13	0.20	1.04	[0.86,1.26]	0.06	0.08	-0.10	0.23	1.08	[0.89,1.30]