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Maud Marsot, Célia Bernard, Ariane Payne, Sophie Rossi, Sandrine Ruelle, et al.. “BACACIX”, a spatial index combining proxies of bovine and badger space use associated with extended *Mycobacterium bovis* circulation in France. *Preventive Veterinary Medicine*, 2023, 211, pp.105817. 10.1016/j.prevetmed.2022.105817 . hal-03918300

HAL Id: hal-03918300

<https://hal.science/hal-03918300>

Submitted on 27 Feb 2023

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“BACACIX”, a spatial index combining proxies of bovine and badger space use associated with extended *Mycobacterium bovis* circulation in France.

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Research Paper

1 “BACACIX”, a spatial index combining proxies of bovine and badger space use associated with extended
2 *Mycobacterium bovis* circulation in France

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7 **Research Paper**

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12 **Highlights**

13 We designed and calculated a spatial index of indirect cattle–badger contacts in France, named “BACACIX”.

14 The index combined spatial models of land use distribution for both species.

15 High values for the index were found along two geographical axes in France.

16 In two areas, index values were low, suggesting unlikely indirect contacts.

17 A model showed that the index was associated with the risk of cattle bTB outbreaks.

18

19 **Abstract**

20 To better prevent and control multi-host pathogen circulation over large areas, it is essential to identify patterns
21 of disease persistence within host communities involved in pathogen circulation at a macroscale. The aim of
22 this study was to design and calculate “BACACIX”, a spatial index of indirect contacts between cattle and
23 badgers, two species involved in the circulation of *Mycobacterium bovis*, one of the main causative agents of
24 bovine tuberculosis, in some areas of France. The index combined spatial models of land use distribution (the
25 probable distribution defining animal use of space) based on pasture location for cattle, and based on land
26 cover for badgers, with proxies for animal density for both species. For badgers, we used two series of census
27 data of badger setts in two regions of France to evaluate our model of badger space use distribution (also
28 known as utilization distribution), and analyzed the relationship between BACACIX and the upsurge of bovine
29 tuberculosis (bTB) observed in several regions of France during the decade after the country obtained the
30 officially bTB-free status in 2001. We observed high values of BACACIX from the southwest to the northeast
31 of France and from Brittany to the Channel coast. Conversely, in two areas (north-central area and
32 Mediterranean coast), index values were low, suggesting that indirect cattle–badger contacts were unlikely. In
33 the two series of census data of badger setts that we analyzed, 96.5% and 87% of the global positioning system
34 (GPS) locations of badger setts, respectively were located in the calculated badger space use distribution. A
35 logistic regression model showed that after controlling bTB over the previous decade, the value of the index
36 was positively associated with the risk of cattle outbreaks between 2001 and 2010 (OR = 1.57). In addition,
37 the risk of bTB occurrence in cattle decreased when the pasture area outside the badger space use distribution
38 increased. In the future, the spatial index of indirect cattle–badger contacts we propose could help to better
39 target bTB surveillance and control in France.

40

41 **Keywords:** BACACIX , cattle, badger, bovine tuberculosis

42

43 **Introduction**

44 Many infectious diseases can affect multiple species of domestic or wild animals, as well as humans
45 (Cunningham et al., 2017). Understanding the transmission ecology of multi-host pathogens has been
46 highlighted as one of the major challenges in biomedical sciences for the 21st century (Woolhouse et al., 2001).
47 Interspecific pathogen transmission between populations is frequently complex (Yon et al., 2019), with
48 multiple transmission routes (Webster et al., 2017), and contacts occurring simultaneously or sequentially.
49 Examples of complex transmission routes include those of agents responsible for bovine tuberculosis (bTB,
50 Yon et al., 2019), African swine fever (Gavier-Widen et al., 2020) and Rift Valley fever (Clark et al., 2018).

51 To better prevent and control infectious diseases at the wildlife-livestock interface, it is essential to
52 determine the risk of disease transmission between host populations, by assessing how individuals use their
53 environment and how the environment affects interspecific interactions (Barasona et al., 2014). Direct and
54 indirect contacts between sympatric species favor the spread of pathogens (Claas et al., 1998; Frolich et al.,
55 2002; Gortázar et al., 2007; Barth et al., 2018). The frequency of these contacts depends on the abundance of
56 hosts and on their habitat use in relation to landscape structure (presence of forests, woods, hedges, etc.) This
57 structure drives the presence of favorable environments for interactions between the different species involved
58 in the multi-host system. In the United Kingdom, there is concern that deer populations may play a greater role
59 in *M. bovis* persistence in the future, with spillback transmission to cattle through land sharing, as deer
60 abundance is increasing and their range is expanding (Bohm et al., 2007). Wildlife habitat use and selection
61 are determined by ecological processes, such as animal movement, use of habitat, reproduction, diet or social
62 interactions, and environmental factors, such as resource availability and habitat configuration (Jacquier et al.,
63 2020). Predictions of spatial abundance patterns over large areas remain scarce for many taxa (Sagarin et al.,
64 2006). For hunted species, statistical models based on hunting bag data can be used to derive reliable estimates
65 of relative abundance at a broad scale (e.g. for wild boars, see Acevedo et al., 2014; Ruiz-Rodríguez et al.,
66 2022). Most field and statistical methods rely on complex designs to estimate local absolute abundance, and
67 are inapplicable or too expensive to be considered for abundance estimation in large spatial scale studies
68 (Jacquier et al., 2020). Relative abundance estimates allow for the study of species over broad spatial scales,
69 under the assumption that the population index is proportional to the population density (Pollock et al., 2002).

70 Many tools are available to estimate direct and/or indirect contacts between domestic and wildlife
71 species involved in multi-host pathogen circulation (Schauber et al., 2007; Vourc'h et al., 2008; Brook and

72 McLachlan, 2009; Barasona et al., 2014; zu Dohna et al., 2014; Payne et al., 2018; Bacigalupo et al., 2020).
73 These tools, mainly developed at a local scale (e.g., motion-activated cameras, global positioning system (GPS)
74 collars, questionnaires, etc.), are useful to assess spatiotemporal interactions and their implications for
75 pathogen transmission. Moreover, many studies in community ecology evaluate species association indices
76 (de Caceres and Legendre, 2009; Jesus et al., 2018; Auffret and Thomas, 2019), with for example the *phi*
77 *coefficient of association*, the *indicator value index* and the *beta diversity index*. These concepts can be used
78 in epidemiology to identify areas at risk of interspecific contacts that facilitate the circulation of multi-host
79 pathogens. Interest in quantifying home-range overlap or space-use sharing between animals has increased in
80 recent years in ecology (Kernohan et al., 2001; Fieberg et al., 2005; Weterings et al., 2019). When examining
81 the interface between species, Fieberg et al. showed that the indices commonly used to quantify home-range
82 overlap (e.g., space-use sharing among individuals) have certain limitations and suggested that new overlap
83 indices using space use distribution were likely more informative (Fieberg et al., 2005). This concept, called
84 space use distribution in this article, is the probable distribution defining the animal's use of space. When
85 simultaneous observations of animal locations are available, it is possible to assess the degree of dynamic
86 interaction between individuals. However, the most common situation corresponds to static interaction analysis
87 in which sets of individual locations are compared without reference to the temporal sequence of these
88 locations (Kernohan et al., 2001; Fieberg et al., 2005). This type of tool may be useful to characterize the
89 wildlife-livestock interface in ecosystems where multi-host pathogens circulate, such as *M. bovis* (Gortazar et
90 al., 2014).

91 France was recognized as officially bTB-free in 2001 (Decision 2001/26/EC), after 6 years with a herd
92 prevalence rate of <0.1%. However, an upsurge in bTB outbreaks was observed from 2004 in various
93 departments. A low level of *M. bovis* circulation persisted in several areas, with about a hundred cattle
94 outbreaks per year and circulation between domestic and wild hosts (Palisson et al., 2016). In France, cases of
95 *M. bovis* in wildlife were identified for the first time in 2001. The *M. bovis* wild host community in the country
96 comprises badgers, wild boar, deer (*Cervus elaphus* and *Capreolus capreolus*), and foxes. Infected wildlife
97 hosts have always been found near infected cattle (Reveillaud et al., 2018). In France, the epidemiologic roles
98 of the different wildlife hosts depend on the species and the local context (Payne et al., 2012; Lambert et al.,
99 2016; Reveillaud et al., 2018; Richomme et al., 2020). Direct contacts between cattle and badgers have been
100 shown to be very rare (Mullen et al., 2013; Mullen et al., 2015; Payne et al., 2016; Campbell et al., 2019;

101 Varela-Castro et al., 2021; Woodroffe et al., 2021), and *M. bovis* inter-species transmission is rather considered
102 to be environment-mediated, since this pathogen may survive for several months in the soil (Fine et al., 2011;
103 Barbier et al., 2017). Bouchez-Zacria et al. (2018) showed that the distribution of bTB in cattle herds in south-
104 western France was partly linked to badger-mediated contact networks. As fragmented landscapes and pastures
105 are often part of the badger habitat, we made the hypothesis that a high interspecific contact risk between cattle
106 and badgers can be assumed at the forest-pasture interface (Roper, 2010; Bouchez-Zacria et al., 2017).

107 To characterize the cattle-wildlife interface and given that there is no consensus definition for this
108 concept that encompasses the quantification of space sharing between species, we developed a spatial index
109 of indirect contact between species based on Fieberg's concept of utilization distribution (space use
110 distribution) (Fieberg et al., 2005). The aim of this work was to propose and calculate a spatial index of indirect
111 contacts between cattle and badgers, based on two assumptions: (i) the occurrence of indirect contacts is
112 spatially limited to the overlap between the space use distributions of both species, and (ii) the level of
113 abundance of both species influences the frequency of contacts. We used two series of census data for badger
114 setts in two different regions of France to evaluate our model of badger space use distribution. Finally, we
115 analyzed the relationship between the proposed spatial index and the upsurge of bTB observed in several
116 regions during the decade 2001-2010, after France obtained the officially bTB-free status.

117

118 **Materials and Methods**

119 *Data*

120 Cattle farms data.

121 We extracted from the French cattle tracing system database (i) the number of cows (i.e., female cattle
122 after first calving) as of 2016-07-01, by breed category (dairy or beef), for the 153,865 cattle farms (excluding
123 overseas territories and Corsica), and (ii) the municipality where the farm was located. Using the land
124 registration system, we prepared a geographic information system (GIS) layer containing the 3,036,515 land
125 plots used as permanent pastures, based on data provided by farmers to claim EU Common Agricultural Policy
126 (CAP) subsidies in 2014 (Palisson et al., 2017). For confidentiality reasons, the identity of farmers had been
127 anonymized in the database we accessed, and there was no connection between the anonymous farmer ID in
128 the land registration system and the farm ID in the cattle tracing system. As a result, the connection between

129 land registration data and the cattle tracing system could not be established at the farm level (due to the
130 anonymization of land registration data), but at the municipality level.

131 Land cover and badger data.

132 Land cover data were extracted from the BD TOPO Vegetation[®] database from 2016 and provided by
133 the French National Institute of Geographic and Forest Information (IGN). The nomenclature used in this
134 database describes the types of vegetation found in mainland France and overseas territories.

135 Census data on badger setts are available for several regions of France, as part of bTB control
136 measures. We used the datasets generated in two censuses, one in southwestern France (Pyrénées-Atlantiques
137 [PA] and Landes departments), and one in the center of the country (Côte d'Or department). The PA-Landes
138 dataset contained the GPS locations of 2,856 badger setts (Bouchez-Zacria et al., 2017). The Côte d'Or dataset
139 contained 1,738 GPS locations of badger setts, or badger trapping sites (Bouchez-Zacria et al., in progress).

140 Bovine tuberculosis data.

141 The annual incidence of bTB, i.e., the number of newly reported infected herds in a given year, was
142 obtained from the French Ministry of Agriculture for each of the 95 departments (the third level in the EU
143 nomenclature of territorial units for statistics) of mainland France, between 1991 and 2010 (see Bekara et al.,
144 2016 for details on this dataset).

145

146 *Spatial index of indirect contacts between cattle and badgers*

147 Definition of BACACIX

148 For both species, we modeled the space use distribution of animals by a uniform distribution inside a
149 set of patches (i.e., spatial polygons) denoted below \mathcal{P}_{sp} with $sp \in \{ct, bg\}$ (ct for cattle, and bg for badger).
150 In a given area z , we quantified the frequency of indirect contacts between cattle and badgers using the
151 following index, named BACACIX (for BAdger-CAttle Contact IndeX):

$$152 \quad \mathcal{C}_{bg,ct}(z) = \mathcal{D}_{bg}(z) \mathcal{D}_{ct}(z) \sum_{p \in \mathcal{P}_{bg}} \sum_{q \in \mathcal{P}_{ct}} |z \cap p \cap q| \quad (1)$$

153 where $\mathcal{D}_{sp}(z)$ is the density of animals of species sp in patches of \mathcal{P}_{sp} in area z , $x \cap y$ is the spatial intersection
154 between polygons x and y , and $|x|$ is the surface of polygon x .

155 Relative density of badgers

156 Badgers can occupy a large range of habitats, such as woodlands, forests, and to a lesser extent arid or
157 mountainous landscapes (Griffiths and Thomas, 1993). Using the nomenclature of the BD TOPO Vegetation[®]

158 database, we first selected the six vegetation types where badger primary setts are generally found in France:
 159 deciduous forest, coniferous forests, mixed forest, open forest, hedge, woods, and wooded area (Jacquier et
 160 al., 2021). We then merged contiguous patches, and excluded the most isolated and small ones ($<10^4$ m²). The
 161 result of this calculation is referred below as the "badger vegetation patch set". Field observations and expert
 162 opinions suggest that badger tracks and secondary setts are mainly observed around 200 m of vegetation
 163 patches of the above types, and within 100 m within them (Kruuk, 2009). We therefore calculated a second set
 164 of land patches by drawing 200 m buffer zones around patches of the badger vegetation patch set, while
 165 deleting the internal areas located more than 100 m from the outer boundary of the patch (Figure 1). The result
 166 of this calculation, denoted \mathcal{P}_{bg} in formula (1), corresponded to the modeled badger space use distribution.
 167 The relative density of badgers in patches of \mathcal{P}_{bg} was derived from the relative abundance estimated by
 168 Jacquier et al. from data collected between 2006 and 2009 in the "small agricultural regions" of France: groups
 169 of neighboring municipalities having similar landscapes and agricultural practices (Jacquier et al., 2020). The
 170 relative density of badgers in patches of \mathcal{P}_{bg} , in a given area z , was calculated by:

$$171 \quad \mathcal{D}_{bg}(z) = \frac{1}{\sum_{p \in \mathcal{P}_{bg}} |z \cap p|} \sum_{r \in SAR} B_r \frac{\sum_{p \in \mathcal{P}_{bg}} |z \cap r \cap p|}{\sum_{p \in \mathcal{P}_{bg}} |r \cap p|}$$

172 where SAR is the set of small agricultural regions, and B_r the relative badger abundance in the small agricultural
 173 region r according to Jacquier et al. (2020).

174 Cattle density

175 We assumed cattle could only be located on pastures: \mathcal{P}_{ct} was the set of patches of permanent and temporary
 176 grasslands, according to the land registration system. As previously explained, the connection between land
 177 registration data and the cattle tracing system was established at the municipality level. For the calculation, we
 178 assumed that the animals on farms of a given municipality were uniformly distributed on pastures owned by
 179 farmers in that municipality. Considering that a given farmer could own pastures in several municipalities, we
 180 calculated the density of cattle on pastures in a given area z as follows:

$$181 \quad \mathcal{D}_{ct}(z) = \frac{1}{\sum_{p \in \mathcal{P}_{ct}} |z \cap p|} \sum_{j \in LRS} \sum_{p \in \mathcal{P}_{ct}} |z \cap p| \mathbf{1}_{F(p)=j} \left[\frac{\sum_{i \in CTS} N_i \mathbf{1}_{Mun(i)=Mun(j)}}{\sum_{p \in \mathcal{P}_{ct}} |p| \mathbf{1}_{Mun(F(p))=Mun(j)}} \right]$$

182 where $\mathbf{1}_{cond}$ is the indicator function returning 1 if $cond$ is true and 0 otherwise, and:

- 183 - LRS is the set of (anonymized) farms in the land registration system and CTS the set of farms in the
- 184 cattle registration system;

- 185 - N_x is the number of cows (considered a proxy of herd size) in farm x according to the cattle tracing
 186 system;
- 187 - $F(p)$ is the (anonymized) farm whose owner had declared the grassland parcel p in the land registration
 188 system; and
- 189 - $Mun(x)$ is the municipality where farm x was located. Since the municipality for the farms was not
 190 available in the land registration database, we assumed that $Mun(x)$ was the municipality where the
 191 farmer had declared most of their grassland plots:

$$Mun(x) = \operatorname{argmax}_{m \in \mathcal{M}} (\sum_{p \in \mathcal{P}_{ct}} |m \cap p| 1_{F(p)=x})$$

192 with \mathcal{M} the set of French municipalities.

194 In the above expression, $\sum_{i \in \mathcal{CTS}} N_i 1_{Mun(i)=Mun(j)}$ is the total number of cows on farms of municipality
 195 $Mun(j)$, and $\sum_{p \in \mathcal{P}_{ct}} |p| 1_{Mun(F(p))=Mun(j)}$ the total surface of grasslands owned by farmers of the same
 196 municipality. The ratio of both terms is therefore the density of cows on pastures owned by farmers of $Mun(j)$.
 197 The combination of these densities with plot surfaces, and the sum over all the farms in the land registration
 198 system, finally enables calculation of the density of animals in pastures of area z .

199 We used the GDAL/OGR 3.0.4 library for Python 3.8.10, and R 3.6.1 (R Core Team, 2020). We used
 200 QGIS[®] software (6.4.3) to map the geographic variations of $\mathcal{C}_{bg,ct}$ at the municipality level, using five classes
 201 according to the following percentiles: 0–25%, 25–50%, 50–75%, 75–90% and 90–100%. Three maps were
 202 thus built, one considering, for the calculation of cattle density, $\mathcal{D}_{ct}(z)$: (i) all cows regardless of breed, (ii)
 203 cows of dairy breeds, and (iii) cows of beef breeds.

204

205 *Comparison with ecological and epidemiologic data*

206 We used the two badger datasets to check whether these field observations were consistent with the
 207 model of badger space use distribution we used. For each of the two datasets, we calculated the proportion of
 208 GPS coordinates located in one of the patches of \mathcal{P}_{bg} and, for setts located elsewhere, we computed the distance
 209 to the nearest patch edge of \mathcal{P}_{bg} .

210 We used multivariable logistic regression models to analyze the link between the upsurge of bTB
 211 outbreaks from 2001 and BACACIX, at the department level. The response variable was the number of years
 212 with and without bTB outbreaks in each department between 2001 and 2010 (i.e., a binary variable of bTB

213 occurrence in a given year, grouped by department). The first explanatory variable was $C_{bg,ct}$, calculated for
214 each department using formula (1). Badger density is thought to have been stable overall in France between
215 2006 and 2009 , and we assumed that land cover also remained stable at the department level between 2001
216 and 2010. Conversely, the number of cattle herds has been decreasing regularly since 1965 (Bekara et al.,
217 2016), with a 34% reduction from 263,284 to 173,941 herds between 2004 and 2017 (Canini and Durand,
218 2020). In the calculation of $C_{bg,ct}$, for the density of cattle on pastures ($\mathcal{D}_{ct}(z)$), we used the total number of
219 cattle in 2001 (the number of cows specifically was not available for that year). A second explanatory variable
220 was included in the model to control for the department bTB incidence prior to 2001: the number of years with
221 outbreaks in the ten preceding years (1991–2000). Finally, to control for other sources of *M. bovis* infection
222 on pastures, we included a third explanatory variable: the number of cattle using pastures outside the badger
223 space use distribution, calculated for a given department z by:

$$224 \quad \mathcal{D}_{ct}(z) \left[\sum_{p \in \mathcal{P}_{ct}} |z \cap p| - \sum_{q \in \mathcal{P}_{bg}} |z \cap q| \right].$$

225 To further analyze the relationship between BACACIX and the resurgence of bTB after 2001, we used
226 a second multivariable logistic regression model with the same response variable (number of years with and
227 without bTB outbreaks in each department between 2001 and 2010), but where the explanatory variables were
228 the different components of BACACIX, i.e. the density of cattle, the density of badgers and the spatial
229 intersection between space use of both species,. These components were (i) the relative density of badgers, (ii)
230 the density of cattle on pastures, and (iii) the total surface where cattle and badger space use distribution
231 overlapped. As in the preceding model and for the same reasons, we added as explanatory variables the number
232 of years with outbreaks in 1991–2000, and the total surface of pastures that did not overlap with badger
233 distribution. For both logistic regression models, we checked the absence of multi-collinearity between
234 explanatory variables by verifying that the variance inflation factor was <5 for each of the predictors (Fox and
235 Weisberg, 2018). No variable selection procedure was performed. The quality of model fit was evaluated by
236 computing the area under the receiver-operating curve (AUC).

237

238 **Results**

239 *Geographic variations of BACACIX*

240 Pastures used by cattle were heterogeneously distributed, with the highest density of pastures (at the
241 municipality level) mainly located in the center of France and in Brittany (Figure 2A). According to the model,
242 the space use distribution of badgers was very widespread, with patches frequently observed across the country,
243 with the exception of north-eastern France (Figure 2B). The density of cows on pastures (Figure 2C) was the
244 highest in Brittany, where the number of animals was high, and in the northern part of the country (Hauts-de-
245 France region), where the density of pastures was low (Figure 2A). Despite the high number of animals in the
246 central part of the country, the density of cows on pastures was moderate due to the high density of pastures
247 in this area (Figure 2C). We observed very low densities of cows in Ile-de-France, on the southeast coast, and
248 on the Mediterranean rim. The density of dairy cows was high in Brittany and northern France (Appendix 1A),
249 while the highest beef cows density was in central France (Appendix 1B). According to the model, inside their
250 space use distribution area (shown in Figure 2B), the relative density of badgers was lower in Brittany, in parts
251 of central France, and in the southeastern part of the country (Figure 2D).

252 The geographic variations of BACACIX are shown in Figure 3. We observed two axes where the index
253 was high, a first one along a southwest to northeast axis of France, and a second one from Brittany to the
254 Channel coast. In two parts of the country (north-central and Mediterranean coast), the index was low. Similar
255 geographic variations were observed for dairy (Appendix 2A) and beef cows (Appendix 2B), with higher
256 values of BACACIX from Brittany to the Channel coast for dairy cows, and from southwest to northeast for
257 beef cows.

258

259 *Comparison with ecological and epidemiologic data*

260 In the PA-Landes dataset, 96.5% of the 2,856 GPS locations of badger setts were located in patches of
261 the badger space use distribution (\mathcal{P}_{bg}). Most of these setts ($n = 2,699$, 94.5%) were located inside one of the
262 patches of the badger vegetation patch set. For the 3.5% of setts located outside the badger space use
263 distribution ($n = 100$ setts), the median distance to the nearest patch of \mathcal{P}_{bg} was 157 m. In the Côte d'Or dataset,
264 87% of the 1,738 setts or trapping sites ($n = 1,511$) were located inside one of the patches of \mathcal{P}_{bg} . Like in PA-
265 Landes, most of these GPS locations (84%) were located inside a patch of the badger vegetation patch set. The
266 227 trapping sites and setts located outside patches of \mathcal{P}_{bg} were at a median distance of 148 m from the nearest
267 patch (Figure 4).

268 The multivariable logistic regression model of the risk of bTB outbreak occurrence in a department
269 between 2001 and 2010 showed a significant and positive effect of BACACIX on the risk of outbreak
270 occurrence ($p=0.002$). The corresponding odds-ratio (OR) was 1.57 when the index was increased by the inter-
271 quartile range of its distribution. As expected, previous bTB history in the department (number of years with
272 bTB outbreaks in 1991–2000) was also significantly associated with the risk of outbreak occurrence. The
273 number of cattle using pastures outside the badger space use distribution was associated with a decreased risk
274 of bTB occurrence (Table 1). When analyzing the effects of the different components of BACACIX separately,
275 we found significant effects of (i) the surface of pasture shared by cattle and badgers, which increased the risk
276 of outbreak occurrence (OR: 1.52), and (ii) cattle density, which decreased this risk (OR: 0.71). Badger density
277 was not associated with the risk of outbreak occurrence. As in the previous model, we observed a significant
278 negative effect of local bTB history (1991–2000) and a protective effect of the total surface of pasture used by
279 cattle but not by badgers (Table 2). The AUC was 0.80 for the first model and 0.85 for the second one,
280 indicating good quality of the model fit to data in both cases.

281

282 **Discussion**

283 As many pathogens can circulate at the interface between populations of cattle and wildlife (i.e., the
284 space shared by both wild and domestic hosts), estimating the level of contacts between herds and populations
285 of wild species is useful to better understand multi-host pathogen transmission (Cooper et al., 2010). This
286 analysis is also critical for designing targeted control strategies. The objective of this study was to design and
287 calculate BACACIX, a spatial index of indirect contacts between cattle and badgers, two species involved in
288 the circulation of *M. bovis* in France. We observed high values of BACACIX from southwest to northeast and
289 from Brittany to the Channel coast, which could be explained by the high density of cattle and the favorable
290 environment for badger establishment in these areas (landscape of bocage, high concentration of hedgerows).
291 Conversely, we observed lower values of the index in the north-central part of the country, due to a lower
292 density of pastures and of favorable environment for badger. The low values of the index along the
293 Mediterranean coast were rather explained by low densities of cattle and badger. Additionally, areas where *M.*
294 *bovis* circulates in France (e.g., in the southwest) correspond to high values of the index, and we showed that
295 BACACIX we propose has good predictive capacity to estimate the bTB risk in France at the department and
296 decade levels. As a result, this spatial index could be used to draw risk maps at a national or department level.

297 BACACIX is based on models of the space use distribution for both species, and on proxies for the
298 densities of cattle and badgers. This index could have been calculated more accurately if we had access to non-
299 anonymized data. Concerning the model of badger space use distribution, the lower proportion of badger setts
300 in the badger space use distribution in the Côte d'Or dataset (87%) compared to the PA-Landes dataset (96.5%)
301 is probably related to differences in the nature of the data they contained. For Côte d'Or, some of the GPS data
302 corresponded to locations of badger trapping and some to sett locations. Conversely, in the PA-Landes, all
303 GPS data corresponded to sett locations. Moreover, as the two censuses of badger setts did not allow us to
304 differentiate primary and secondary badger setts, we were not able to focus only on primary setts (i.e., the main
305 badger setts), although the model of space use distribution was based on the vegetation types where primary
306 setts are most usually established. However, we observed good consistency between field data and the modeled
307 badger space use distribution. Further studies are needed to assess the predictive ability of this distribution for
308 the presence of badger setts.

309 It would be interesting to adapt BACACIX of indirect contact evaluated at the municipality scale to a
310 local scale such as cattle pastures, with the objective of prioritizing biosecurity measures by precisely
311 identifying the pastures at risk of interspecific contact. However, working at this finer scale would imply taking
312 into account local spatial and temporal variations in space use and the density of populations of the species
313 considered. Moreover, it would be important to consider the risk of interspecific contact not only on cattle
314 pastures but also in farm buildings, since most cattle are housed in winter, even though field studies indicate
315 that the presence of badgers inside farm buildings is rare in France. For instance, in this study, we did not
316 consider seasonal variations in the use of pastures. As some studies have produced different contact risk maps
317 between seasons (Schauber et al., 2007; Brook and McLachlan, 2009; Payne et al., 2018), a dynamic interface
318 analysis at a local scale would be beneficial and informative, if simultaneous measurements are available for
319 the different species (Fieberg et al., 2005). In Spain, the frequency of interactions between wild boars and
320 cattle was significantly higher during spring and autumn, probably owing to higher individual aggregation
321 around shared resources (Barasona et al., 2014; Triguero-Ocana et al., 2019). In France, different livestock
322 husbandry practices than static ones, such as pastoralism and transhumance, induce variability in the presence
323 of cattle on pastures, depending on the season. As a result, here, the densities of cattle could be overestimated
324 in mountainous areas during winter for example, biasing the estimation of BACACIX in these areas. The
325 seasons influence not only cattle grazing but also the behavior of wildlife. Importantly, badger space use

326 distribution is not temporally homogenous: badgers hardly leave their setts in winter, often occupy a larger
327 home-range in spring and may use secondary setts especially in summer, but also during other seasons
328 depending on age and reproduction (Roper, 2010). The estimated BACACIX therefore seemed to be more
329 accurate for spring and autumn, especially when considering BACACIX at a local scale. It would be interesting
330 to differentiate the estimates of density between seasons to improve evaluation of the index.

331 This preliminary study attempted to evaluate indirect contacts between cattle and badgers in France,
332 with the aim of identifying interspecific contact areas, which are potential risk areas for the transmission of *M.*
333 *bovis*. Using a logistic regression model, we showed that BACACIX was associated with large-scale
334 (department level) and long-term (decade) *M. bovis* transmission, whether in the overall analysis or by
335 considering the different components of the index separately. However, the risk of bTB occurrence in cattle
336 decreased when the area of pasture outside the badger space use distribution increased. The results show high
337 reliability because the area under the receiver-operating curve indicated good quality of the model fit to data.
338 These results are consistent with previous studies carried out in France, suggesting a role of the badger in the
339 bTB multi-host system in the country, and especially between cattle and badgers (Payne et al., 2016; Bouchez-
340 Zacia et al., 2017; Bouchez-Zacia et al., 2018). We found no effect of the relative density of badgers on the
341 risk of bTB occurrence in cattle, suggesting that the overlap between cattle and badger space use distributions
342 is more important than the density taken alone. To go further, it would be interesting to validate the link between
343 the presence of bTB and the risk index at a finer scale. Clearly, other components such as landscape factors
344 (humidity, soil type, or vegetation cover) (humidity, soil type or vegetation cover, Barbier et al., 2017;
345 Bouchez-Zacia et al., 2017) may influence the persistence of *M. bovis* in the environment and consequently,
346 the indirect transmission between hosts. Validating the risk of indirect contacts, at a small scale, could be
347 achieved with several approaches: (i) biomarkers such as the microbiota of domestic and wild species (Barth
348 et al., 2018), (ii) questionnaires to farmers dealing with presence of wildlife on their pastures and farm
349 buildings (Brook and McLachlan, 2009; Payne et al., 2018), GPS data (Barasona et al., 2014), (iii) camera-
350 trapping (Payne et al., 2016; Varela-Castro et al., 2021), or (iv) wildlife track surveys directly in the pastures.
351 The method of biomarkers has been used otherwise for several mammalian species, particularly wild and
352 domestic cattle (Mercat et al., 2015), mustelids (Pesapane et al., 2013), primates (Rwego et al., 2008b) and
353 humans (Rwego et al., 2008a).

354 To conclude, the quantification of the indirect contact between badgers and cattle is complex because
355 it is the result of a multifactorial process (zu Dohna et al., 2014). Although its evaluation at a fine scale requires
356 further investigation, the spatial index we proposed could help focusing bTB surveillance and control
357 measures, based on a better knowledge of the areas of higher level of contacts between cattle and badgers. At
358 a local scale, especially within departments where *M. bovis* circulate, the index could help implementing
359 biosecurity measures adapted to the local situation. Finally, the approach developed in this study, focusing on
360 two species, can be used for other species involved in *M. bovis* multi-host system, encountered in France, such
361 as wild boar or red deer.

362

363 References

- 364 Acevedo, P., Quirós-Fernández, F., Casal, J., Vicente, J., 2014. Spatial distribution of wild boar population abundance: Basic
365 information for spatial epidemiology and wildlife management. *Ecological Indicators* 36, 594-600.
- 366 Auffret, A.G., Thomas, C.D., 2019. Synergistic and antagonistic effects of land use and non-native species on community responses
367 to climate change. *Glob Chang Biol* 25, 4303-4314.
- 368 Bacigalupo, S.A., Dixon, L.K., Gubbins, S., Kucharski, A.J., Drewe, J.A., 2020. Towards a unified generic framework to define and
369 observe contacts between livestock and wildlife: a systematic review. *PeerJ* 8, e10221.
- 370 Barasona, J.A., Latham, M.C., Acevedo, P., Armenteros, J.A., Latham, A.D., Gortazar, C., Carro, F., Soriguer, R.C., Vicente, J., 2014.
371 Spatiotemporal interactions between wild boar and cattle: implications for cross-species disease transmission. *Vet Res* 45,
372 122.
- 373 Barbier, E., Rochelet, M., Gal, L., Boschirolì, M.L., Hartmann, A., 2017. Impact of temperature and soil type on *Mycobacterium bovis*
374 survival in the environment. *PLoS One* 12, e0176315.
- 375 Barth, S.A., Blome, S., Cornelis, D., Pietschmann, J., Laval, M., Maestrini, O., Geue, L., Charrier, F., Etter, E., Menge, C., Beer, M.,
376 Jori, F., 2018. Faecal *Escherichia coli* as biological indicator of spatial interaction between domestic pigs and wild boar (*Sus*
377 *scrofa*) in Corsica. *Transbound Emerg Dis* 65, 746-757.
- 378 Bekara, M.E., Azizi, L., Benet, J.J., Durand, B., 2016. Spatial-temporal Variations of Bovine Tuberculosis Incidence in France between
379 1965 and 2000. *Transbound Emerg Dis* 63, 101-113.
- 380 Bohm, M., White, P.C., Chambers, J., Smith, L., Hutchings, M.R., 2007. Wild deer as a source of infection for livestock and humans
381 in the UK. *Vet J* 174, 260-276.
- 382 Bouchez-Zacria, M., Courcoul, A., Durand, B., 2018. The distribution of bovine tuberculosis in cattle farms is linked to cattle trade
383 and badger-mediated contact networks in South-Western France, 2007-2015. *Front Vet Sci* 5, 173.
- 384 Bouchez-Zacria, M., Courcoul, A., Jabert, P., Richomme, C., Durand, B., 2017. Environmental determinants of the *Mycobacterium*
385 *bovis* concomitant infection in cattle and badgers in France. *European Journal of Wildlife Research* 63.
- 386 Brook, R.K., McLachlan, S.M., 2009. Transdisciplinary habitat models for elk and cattle as a proxy for bovine tuberculosis transmission
387 risk. *Prev Vet Med* 91, 197-208.
- 388 Calenge, C., Albaret, M., Leger, F., Vandell, J.-M., Chadoeuf, J., Giraud, C., 2016. Premières cartes d'abondance relative de six
389 mustélidés en France. *Faune Sauvage* 130.
- 390 Campbell, E.L., Byrne, A.W., Menzies, F.D., McBride, K.R., McCormick, C.M., Scantlebury, M., Reid, N., 2019. Interspecific
391 visitation of cattle and badgers to fomites: A transmission risk for bovine tuberculosis? *Ecol Evol* 9, 8479-8489.
- 392 Canini, L., Durand, B., 2020. Resilience of French cattle farms to bovine tuberculosis detection between 2004 and 2017. *Prev Vet Med*
393 176, 104902.
- 394 Claas, E.C., Osterhaus, A.D., van Beek, R., De Jong, J.C., Rimmelzwaan, G.F., Senne, D.A., Krauss, S., Shortridge, K.F., Webster,
395 R.G., 1998. Human influenza A H5N1 virus related to a highly pathogenic avian influenza virus. *Lancet* 351, 472-477.
- 396 Clark, M.H.A., Warimwe, G.M., Di Nardo, A., Lyons, N.A., Gubbins, S., 2018. Systematic literature review of Rift Valley fever virus
397 seroprevalence in livestock, wildlife and humans in Africa from 1968 to 2016. *PLoS Negl Trop Dis* 12, e0006627.
- 398 Cooper, S.M., Scott, H.M., de la Garza, G.R., Deck, A.L., Cathey, J.C., 2010. Distribution and interspecies contact of feral swine and
399 cattle on rangeland in south Texas: implications for disease transmission. *J Wildl Dis* 46, 152-164.
- 400 Cunningham, A.A., Daszak, P., Wood, J.L.N., 2017. One Health, emerging infectious diseases and wildlife: two decades of progress?
401 *Philos Trans R Soc Lond B Biol Sci* 372.
- 402 de Caceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90,
403 3566-3574.
- 404 Fieberg, J., Kochanny, C.O., Lanham, 2005. Quantifying home-range overlap: the importance of the utilization distribution. *Journal of*
405 *Wildlife Management* 69, 1346-1359.
- 406 Fine, A.E., Bolin, C.A., Gardiner, J.C., Kaneene, J.B., 2011. A Study of the Persistence of *Mycobacterium bovis* in the Environment
407 under Natural Weather Conditions in Michigan, USA. *Vet Med Int* 2011, 765430.
- 408 Fox, J., Weisberg, S., 2018. *An R Companion to Applied Regression*. SAGE Publications.

409 Frolich, K., Thiede, S., Kozikowski, T., Jakob, W., 2002. A review of mutual transmission of important infectious diseases between
410 livestock and wildlife in Europe. *Ann N Y Acad Sci* 969, 4-13.

411 Gavier-Widen, D., Stahl, K., Dixon, L., 2020. No hasty solutions for African swine fever. *Science* 367, 622-624.

412 GDAL/OGR contributors, 2022. GDAL/OGR Geospatial Data Abstraction software Library. Open Source Geospatial Foundation.
413 URL <https://gdal.org>.

414 Gortazar, C., Diez-Delgado, I., Barasona, J.A., Vicente, J., De La Fuente, J., Boadella, M., 2014. The Wild Side of Disease Control at
415 the Wildlife-Livestock-Human Interface: A Review. *Front Vet Sci* 1, 27.

416 Gortazar, C., Ferroglio, E., Höfle, U., Frölich, K., Vicente, J., 2007. Diseases shared between wildlife and livestock: a European
417 perspective. *European Journal of Wildlife Research* 53.

418 Griffiths, H.I., Thomas, D.H., 1993. The status of the Badger *Meles meles* (L., 1758) (Carnivora, Mustelidae) in Europe. *Mammal*
419 *Review* 23, 17-58.

420 Hudson, P.J., Rizzoli, A., Grenfell, B.T., Heesterbeek, H., Dobson, A.P., 2002. The Ecology of Wildlife Diseases.

421 Jacquier, M., Calenge, C., Say, L., Devillard, S., Ruetten, S., 2020. Altitude shapes the environmental drivers of large-scale variation in
422 abundance of a widespread mammal species. *Ecol Evol* 10, 119-130.

423 Jacquier, M., Vandel, J.M., Leger, F., Duhayer, J., Pardonnet, S., Say, L., Devillard, S., Ruetten, S., 2021. Breaking down population
424 density into different components to better understand its spatial variation. *BMC Ecol Evol* 21, 82.

425 Jesus, S., Pedro, W.A., Bispo, A.A., 2018. Bird diversity along a gradient of fragmented habitats of the Cerrado. *Anais da Academia*
426 *Brasileira de Ciencias* 90, 123-135.

427 Kernohan, B.J., Gitzen, R.A., Millsap, J.J., 2001. Analysis of Animal Space Use and Movements. In: Millsap, J.J., Marzluff,
428 J.M. (Eds.), *Radio Tracking and Animal Populations*. Academic Press, San Diego, 125-166.

429 Kruuk, H., 2009. Spatial organization and territorial behaviour of the European badger
430 *Meles meles*. *Journal of Zoology* 184, 1-19.

431 Lambert, S., Hars, J., Réveillaud, E., Moyon, J.-L., Gares, H., Rambaud, T., Gueneau, E., Faure, E., Boschioli, M.-L., Richomme, C.,
432 2016. Host status of wild roe deer in bovine tuberculosis endemic areas. *European Journal of Wildlife Research* 63.

433 Mercat, M., Clermont, O., Massot, M., Ruppe, E., de Garine-Wichatitsky, M., Miguel, E., Valls Fox, H., Cornelis, D., Andreumont, A.,
434 Denamur, E., Caron, A., 2015. *Escherichia coli* Population Structure and Antibiotic Resistance at a Buffalo/Cattle Interface
435 in Southern Africa. *Appl Environ Microbiol* 82, 1459-1467.

436 Mullen, E.M., MacWhite, T., Maher, P.K., Kelly, D.J., Marples, N.M., Good, M., 2013. Foraging Eurasian badgers *Meles meles* and
437 the presence of cattle in pastures. Do badgers avoid cattle? *Applied Animal Behaviour Science* 144, 130-137.

438 Mullen, E.M., MacWhite, T., Maher, P.K., Kelly, D.J., Marples, N.M., Good, M., 2015. The avoidance of farmyards by European
439 badgers *Meles meles* in a medium density population. *Applied Animal Behaviour Science* 171, 170-176.

440 Palisson, A., Courcoul, A., Durand, B., 2016. Role of Cattle Movements in Bovine Tuberculosis Spread in France between 2005 and
441 2014. *PLoS One* 11, e0152578.

442 Palisson, A., Courcoul, A., Durand, B., 2017. Analysis of the spatial organization of pastures as a contact network, implications for
443 potential disease spread and biosecurity in livestock, France, 2010. *PLoS One* 12, e0169881.

444 Payne, A., Boschioli, M.L., Gueneau, E., Moyon, J.L., Rambaud, T., Dufour, B., Gilot-Fromont, E., Hars, J., 2012. Bovine tuberculosis
445 in "Eurasian" badgers (*Meles meles*) in France. *European Journal of Wildlife Research* 59, 331-339.

446 Payne, A., Chappa, S., Hars, J., Dufour, B., Gilot-Fromont, E., 2016. Wildlife visits to farm facilities assessed by camera traps in a
447 bovine tuberculosis-infected area in France. *European Journal of Wildlife Research* 62, 33-42.

448 Payne, A., Ogweng, P., Ojok, A., Etter, E., Gilot-Fromont, E., Masembe, C., Stahl, K., Jori, F., 2018. Comparison of Three Methods
449 to Assess the Potential for Bushpig-Domestic Pig Interactions at the Wildlife-Livestock Interface in Uganda. *Front Vet Sci*
450 5, 295.

451 Pesapane, R., Ponder, M., Alexander, K.A., 2013. Tracking pathogen transmission at the human-wildlife interface: banded mongoose
452 and *Escherichia coli*. *Ecohealth* 10, 115-128.

453 Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L., Sauer, J.R., 2002. Large scale wildlife monitoring studies:
454 statistical methods for design and analysis. *Environmetrics* 13, 105-119.

455 R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
456 URL <https://www.R-project.org/>.

457 Reveillaud, E., Desvaux, S., Boschioli, M.L., Hars, J., Faure, E., Fediaevsky, A., Cavalerie, L., Chevalier, F., Jabert, P., Poliak, S.,
458 Tourette, I., Hendrikx, P., Richomme, C., 2018. Infection of Wildlife by *Mycobacterium bovis* in France Assessment
459 Through a National Surveillance System, *Sylvatub*. *Front Vet Sci* 5, 262.

460 Richomme, C., Reveillaud, E., Moyon, J.L., Sabatier, P., De Cruz, K., Michelet, L., Boschioli, M.L., 2020. *Mycobacterium bovis*
461 Infection in Red Foxes in Four Animal Tuberculosis Endemic Areas in France. *Microorganisms* 8.

462 Roper, T.J., 2010. *Badger*. Collins London.

463 Ruan, S., 2017. Modeling the transmission dynamics and control of rabies in China. *Math Biosci* 286, 65-93.

464 Ruiz-Rodríguez, C., Fernández-López, J., Vicente, J., Blanco-Aguilar, J.A., Acevedo, P., 2022. Revisiting wild boar spatial models
465 based on hunting yields to assess their predictive performance on interpolation and extrapolation areas. *Ecological Modelling*
466 471.

467 Rwego, I.B., Gillespie, T.R., Isabirye-Basuta, G., Goldberg, T.L., 2008a. High rates of *Escherichia coli* transmission between livestock
468 and humans in rural Uganda. *J Clin Microbiol* 46, 3187-3191.

469 Rwego, I.B., Isabirye-Basuta, G., Gillespie, T.R., Goldberg, T.L., 2008b. Gastrointestinal bacterial transmission among humans,
470 mountain gorillas, and livestock in Bwindi Impenetrable National Park, Uganda. *Conserv Biol* 22, 1600-1607.

471 Sagarin, R.D., Gaines, S.D., Gaylord, B., 2006. Moving beyond assumptions to understand abundance distributions across the ranges
472 of species. *Trends Ecol Evol* 21, 524-530.

473 Schaubert, E.M., Storm, D.J., Nielsen, C.K., 2007. Effects of Joint Space Use and Group Membership on Contact Rates Among White-
474 Tailed Deer. *Journal of wildlife management* 71, 155-163.

475 Triguero-Ocana, R., Barasona, J.A., Carro, F., Sorriquer, R.C., Vicente, J., Acevedo, P., 2019. Spatio-temporal trends in the frequency
476 of interspecific interactions between domestic and wild ungulates from Mediterranean Spain. *PLoS One* 14, e0211216.

477 Varela-Castro, L., Sevilla, I.A., Payne, A., Gilot-Fromont, E., Barral, M., 2021. Interaction Patterns between Wildlife and Cattle Reveal
478 Opportunities for *Mycobacteria* Transmission in Farms from North-Eastern Atlantic Iberian Peninsula. *Animals (Basel)* 11.

479 Voure'h, G., Boyard, C., Barnouin, J., 2008. Mammal and bird species distribution at the woodland-pasture interface in relation to the
480 circulation of ticks and pathogens. *Ann N Y Acad Sci* 1149, 322-325.

481 Webster, J.P., Borlase, A., Rudge, J.W., 2017. Who acquires infection from whom and how? Disentangling multi-host and multi-mode
482 transmission dynamics in the 'elimination' era. *Philos Trans R Soc Lond B Biol Sci* 372.

483 Weterings, M.J.A., Ewert, S.P., Peereboom, J.N., Kuipers, H.J., Kuijper, D.P.J., Prins, H.H.T., Jansen, P.A., van Langevelde, F., van
484 Wieren, S.E., 2019. Implications of shared predation for space use in two sympatric leporids. *Ecol Evol* 9, 3457-3469.

485 Woodroffe, R., Donnelly, C.A., Chapman, K., Ham, C., Moyes, K., Stratton, N.G., Cartwright, S.J., 2021. Successive use of shared
486 space by badgers and cattle: implications for
487 *Mycobacterium bovis*
488 transmission. *Journal of Zoology* 314, 132-142.

489 Woolhouse, M.E., Taylor, L.H., Haydon, D.T., 2001. Population biology of multihost pathogens. *Science* 292, 1109-1112.

490 Yon, L., Duff, J.P., Agren, E.O., Erdelyi, K., Ferroglio, E., Godfroid, J., Hars, J., Hestvik, G., Horton, D., Kuiken, T., Lavazza, A.,
491 Markowska-Daniel, I., Martel, A., Neimanis, A., Pasmans, F., Price, S.J., Ruiz-Fons, F., Ryser-Degiorgis, M.P., Widen, F.,
492 Gavier-Widen, D., 2019. Recent changes in infectious diseases in European wildlife. *Journal of Wildlife Diseases* 55, 3-43.

493 zu Dohna, H., Peck, D.E., Johnson, B.K., Reeves, A., Schumaker, B.A., 2014. Wildlife-livestock interactions in a western rangeland
494 setting: quantifying disease-relevant contacts. *Prev Vet Med* 113, 447-456.

495

Figures

Figure 1: Chart of the spatial intersection between space use distribution of cattle (P_{ct}) and badgers (P_{bg}) in a small zone of the Ain Department (eastern France).



Figure 2: Space use distribution for (A) cattle (P_{ct}) and (B) badgers (P_{bg}) per municipality in France and density of (C) cattle (D_{ct}) and (D) badgers (D_{bg}) per municipality in France. We used four classes of space use distribution and density of cattle and badgers according to the percentiles: 0–25%, 25–50%, 50–75%, and 75–100%. The density of cattle (C) corresponded to the ratio of the total number of cows on farms of a municipality and the total surface of grasslands owned by farmers in the same municipality. The density of badgers (D) corresponded to the ratio of the relative number of badgers (index between 0 and 1) and the total surface of space use distribution (Jacquier et al. 2020).

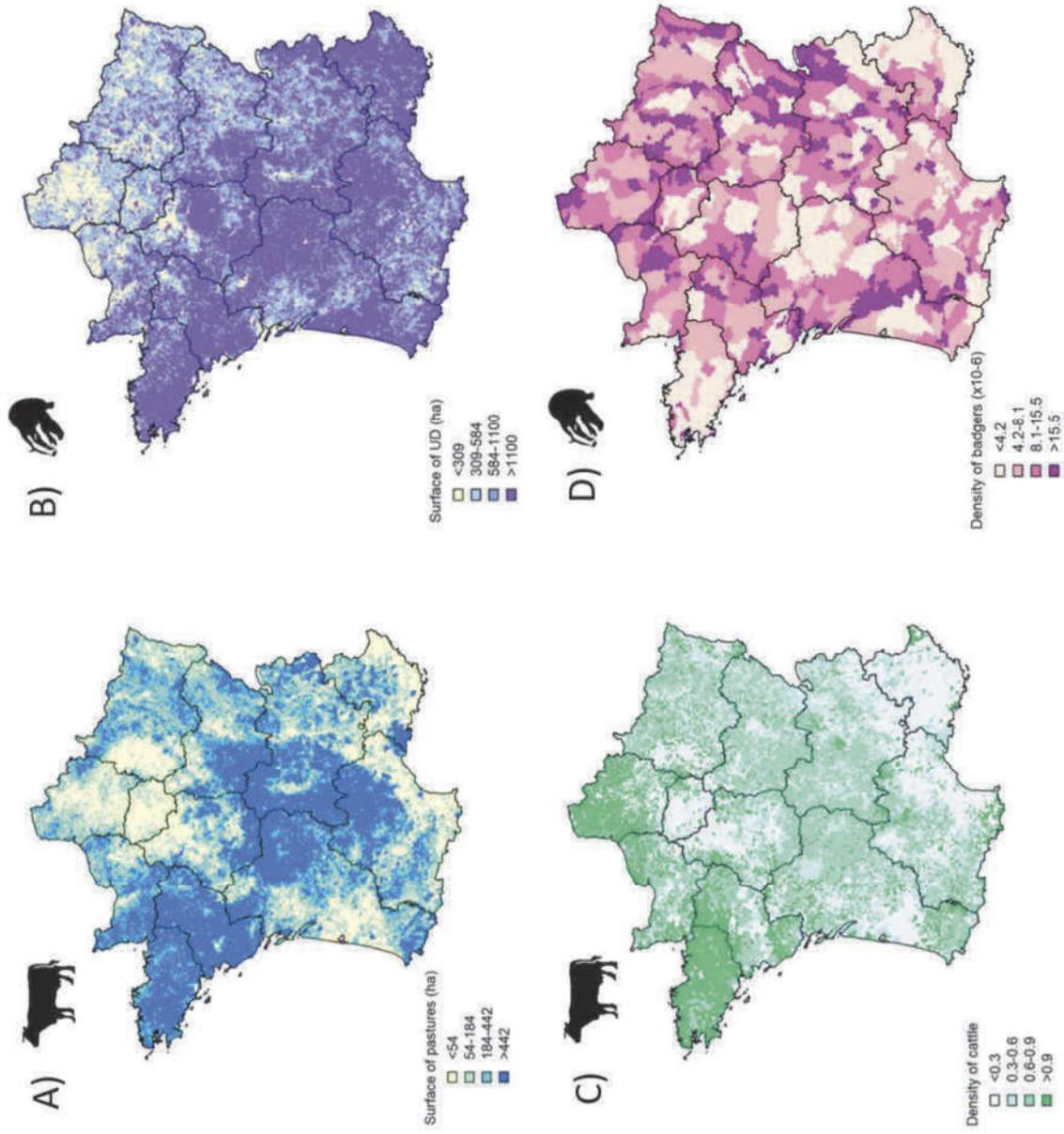


Figure 3: Mapping the spatial index of indirect contacts between cattle and badgers at the municipality scale, i.e., $C_{bg,ct}$ (municipality), in France.

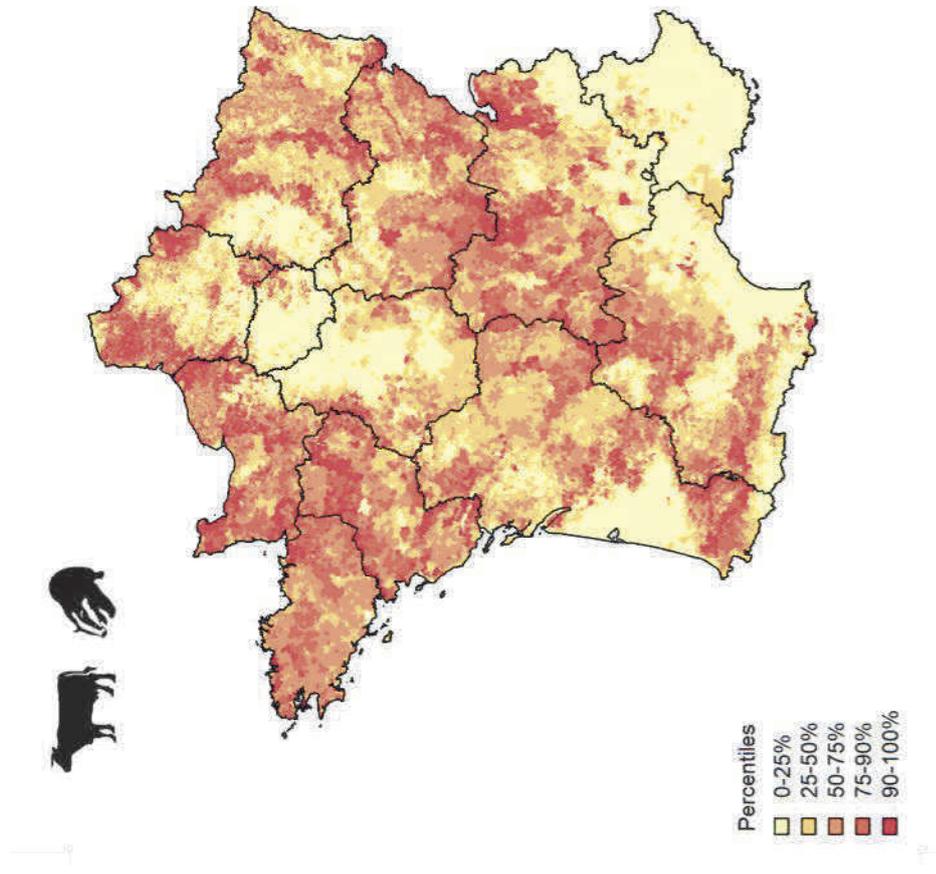
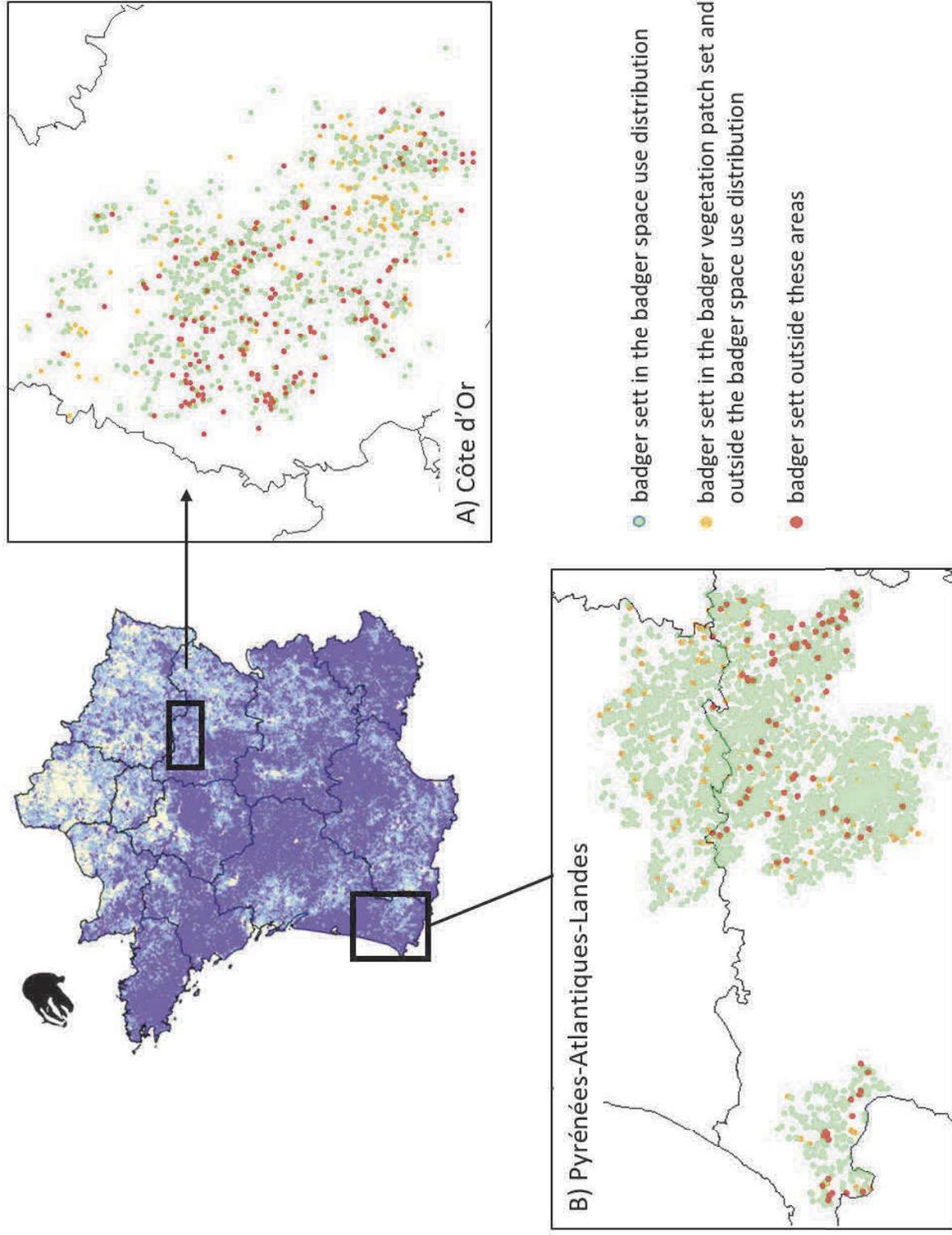


Figure 4: Spatial distribution of geolocated setts in two parts in France, Côte d'Or (A) and Pyrénées-Atlantiques-Landes (B) according to their location in the badger space use distribution (green dots), the badger vegetation patch set (orange dots), and outside these areas (red dots).



Tables

Table 1: Logistic regression model of the risk of bTB occurrence on cattle farms in departments of France between 2001 and 2010, according to the value of the spatial index of indirect contacts between cattle and badgers

Variable	Odds-ratio (95% CI)	p-value
Index of indirect cattle–badger contacts ($C_{bg,ct}$)	1.57 ^a (1.18-2.10)	0.002
Number of years with bTB outbreaks in 1991–2000	1.34 ^b (1.25-1.43)	<0.0001
Number of cattle using pastures not used by badgers	0.56 ^a (0.42-0.75)	<0.0001

^aOdds-ratios obtained when the explanatory variable is increased by the inter-quartile range

^bOdds-ratio corresponding to one more year with bTB outbreaks between 1991 and 2000

Table 2. Logistic regression model of the risk of bTB occurrence on cattle farms in departments of France between 2001 and 2010, according to the different components of the index of indirect contacts between cattle and badgers

Variable	Odds-ratio (95% CI)	p-value
Total surface of pasture shared by cattle and badgers	1.52 ^a (1.28-1.81)	<0.0001
Density of cattle on pastures	0.71 ^a (0.57-0.87)	0.002
Density of badgers on pastures	1.03 ^a (0.86-1.22)	0.75
Number of years with bTB outbreaks in 1991–2000	1.32 ^b (1.24-1.42)	<0.0001
Total surface of pasture used by cattle but not by badgers	0.43 ^a (0.21-0.85)	0.02

^aOdds-ratios obtained when the explanatory variable is increased by the inter-quartile range

^bOdds-ratio corresponding to one more year with bTB outbreaks between 1991 and 2000