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## **Relationships between landscape structure and the prevalence of two tick-borne infectious agents, *Anaplasma Phagocytophilum* and *Borrelia burgdorferi sensu lato*, in small mammal communities**

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27

28

29

30 **Abstract**

31 *Context*

32 By modifying ecosystems, land cover changes influence the emergence, the spread and the incidence  
33 of vector-borne diseases.

34 *Objective*

35 This study aimed at identifying associations between landscape structure and the prevalence of two  
36 tick-borne infectious agents, *Anaplasma phagocytophilum* and *Borrelia burgdorferi* s.l., in small  
37 mammal communities.

38 *Methods*

39 Small mammals were sampled in 24 sites along a gradient of woodland fragmentation and hedgerow  
40 network density, and screened for infectious agents with real-time PCR techniques. For each site,  
41 structural variables (composition and configuration) of the surrounding landscape at various scales (0-  
42 500 m) and variables of wooded habitats connectivity based on graph theory and least cost path  
43 distances for the two dominant species, bank voles (*Myodes glareolus*) and wood mice (*Apodemus*  
44 *sylvaticus*), were computed.

45 *Results*

46 The *A. phagocytophilum* prevalence increased with wooded habitats cover (0-500 m), likely through  
47 host population size, and increased slightly with bank vole abundance, which has a higher reservoir  
48 competence than wood mouse. The *B. burgdorferi* s.l. prevalence increased with wooded ecotones  
49 only at local scales (50-100 m). Wooded habitats connectivity measures did not improve models built  
50 with simple land cover variables. A more marked spatial pattern was observed for the prevalence of  
51 *A. phagocytophilum* than *B. burgdorferi* s.l..

52 *Conclusions*

53 This study highlights the interest of considering together the ecology of infectious agents (e.g. host  
54 specificity) and the host species community ecology to better understand the influence of the  
55 landscape structure on the spatial distribution of vector-borne infectious agents.

56

57 **Keywords**

58 Tick-borne diseases; Small mammal community; Landscape connectivity; Graph theory; Least cost  
59 paths

60

61

62 **Introduction**

63 Landscape changes are suspected to cause infectious disease emergence or reemergence worldwide  
64 (Jones et al. 2008). Several authors depicted the complexity of the interactions between the landscape,  
65 hosts, vectors and humans, which drive the emergence of these diseases (Lambin et al. 2010). The  
66 spread of infectious agents in ecosystems relies partly on their life history traits shaped by their  
67 evolutionary histories (e.g. transmission modalities). Because species within communities exhibit  
68 various levels of reservoir or vector competence, the transmission depends on hosts and vectors  
69 diversity and abundance (Keesing et al. 2009).

70 Landscape structure (composition and configuration), by filtering and regulating richness, abundance  
71 and dispersal of species in hosts and vectors communities, may influence the transmission rate and the  
72 diffusion of infectious agents, which ultimately determine their distribution and prevalence (Suzán et  
73 al. 2015). For instance, an increase in the proportion of non-reservoir hosts may induce an increased  
74 number of missed transmissions between reservoir hosts, or an increased number of wasted bites  
75 (failed transmission events) by vectors. This may reduce the number of transmission events and has a  
76 so called “dilution effect” on prevalence (Ostfeld and Keesing 2000; Clay et al. 2009). Conversely, an  
77 increase in the proportion of competent hosts may increase the number of transmission events or  
78 efficient bites by vectors (Roche et al. 2013). When less competent species are more prone to local  
79 extinction, this non-random species loss in host communities seems to be a driver of the increased  
80 direct and vector-borne infectious disease transmission (Ostfeld and LoGiudice 2003; Johnson et al.  
81 2013; Roche et al. 2013).

82 Habitat connectivity partly shapes hosts community structure. Large-bodied species, with small  
83 clutch/litter size and long gestation/incubation time are supposed to be more sensitive to habitat  
84 fragmentation because they experience higher local extinction risk. Conversely, small-bodied species,  
85 with large clutch/litter size and short incubation/gestation time can persist in fragmented habitat  
86 landscapes. These species need less habitat surface and benefit from a competition and predation  
87 release in these landscapes that are less favorable to predators and specialist species (Nupp and  
88 Swihart 1998, 2000; Gehring and Swihart 2003; Ferrante et al. 2017). As it happens, the latter kind of  
89 species also seem to be better reservoirs for infectious agents (Gottdenker et al. 2012; Huang et al.  
90 2013; Ostfeld et al. 2014). Thus, in fragmented habitat landscapes, one could expect an amplification  
91 of infection prevalence supported by a higher density of more competent hosts (Allan et al. 2003;  
92 Rubio et al. 2014). However, habitat connectivity can also indirectly influence the risk of local  
93 extinction of infectious agents by shaping hosts – and vectors – population size, as demonstrated on  
94 Hantavirus in bank voles (Guivier et al. 2011). Land use is highly changing in Europe (agricultural  
95 intensification in some areas and rewilding in others; Reidsma et al. 2006). Thus, more studies  
96 explicitly assessing how landscape composition, configuration, and the resulting functional

97 connectivity influence interactions and abundances of hosts, vectors and infectious agents to better  
98 understand infectious diseases risk are needed.

99 Small mammals are reservoir hosts of many tick-borne infectious agent taxa: protozoan (e.g. *Babesia*  
100 sp., Hersh et al. 2012), bacteria (e.g. *Borrelia* sp., Gern et al. 1998; *Anaplasma* sp., Stuen et al. 2013)  
101 and viruses (e.g. tick-borne encephalitis virus, Mansfield et al. 2009). Small mammal communities  
102 composition is known to vary according to landscape features like habitat patch size, shape and  
103 isolation (Nupp and Swihart 2000; Michel et al. 2007) and to the constraints that the landscape matrix  
104 imposes on the displacements of small mammals (Szacki et al. 1993).

105 Tick displacements *per se* are reduced and their dispersal occurs mostly while feeding on their hosts  
106 (Araya-Anchetta et al. 2015). Hard ticks (Arthropoda, Arachnida, Ixodidae) need to have a first blood  
107 meal on a vertebrate host to molt from larva to nymph, a second one to molt from nymph to adult then  
108 adult females need a third one to produce eggs once fertilized by adult males. Tick-borne infectious  
109 agents can be acquired by ticks or transmitted to hosts at each blood meal. They disperse either by the  
110 dissemination of ticks getting infected while feeding on infected hosts, or by already infected ticks  
111 while attached on hosts. The dispersal distance of infectious agents depends on home ranges and  
112 competences of tick hosts (Kurtenbach et al. 2002b). Thus, landscape features affecting host  
113 communities and/or their dispersal are of paramount importance in the distribution and the local  
114 prevalence of tick-borne infections.

115 This study focused on *Anaplasma phagocytophilum* and *Borrelia burgdorferi* sensu lato (s.l.). The  
116 *A. phagocytophilum* bacteria ecotype associated to small mammals is transmitted mostly by  
117 *I. trianguliceps* and maybe other endophilic (burrow dwelling) tick species (Bown et al. 2009;  
118 Blaňarová et al. 2014; Jahfari et al. 2014). Infections in small mammals last about a couple of months  
119 (Bown et al. 2003). No transovarial transmission (from engorged females to their offspring) of these  
120 bacteria is known in *Ixodes* ticks (Stuen et al. 2013).

121 In Europe, several genospecies of the *B. burgdorferi* s.l. complex can be hosted by small mammals:  
122 *B. afzelli*, *B. bavariensis* (formerly *garinii* OspA serotype 4 strain), *B. bissetti*, *B. burgdorferi* sensu  
123 stricto (s.s.), and *B. spielmani* (Kurtenbach et al. 2002a, 2006; Margos et al. 2009; Coipan and Sprong  
124 2016). However, host ranges of some of these genospecies include also larger mammals like  
125 hedgehogs (*Erinaceus europaeus*) and squirrels (*Sciurus vulgaris*) (Skuballa et al. 2012; Pisanu et al.  
126 2014). The *B. burgdorferi* s.l. bacteria can be transmitted by several tick species, but the exophilic  
127 (questing for host on the vegetation) tick species *I. ricinus* is assumed to be its main vector in Europe  
128 (Rizzoli et al. 2011). Small mammals are major hosts for *I. ricinus* larvae and only occasional hosts for  
129 nymphs, but they also host endophilic tick species like *I. trianguliceps* and *I. acuminatus* at all life  
130 stages (Boyard et al. 2008; Bown et al. 2008; Hofmeester et al. 2016; Perez et al. 2017). Therefore, the  
131 maintenance of the zoonotic cycle of these bacteria may partly rely on other tick species (Hubbard et  
132 al. 1998; Heylen et al. 2013; Szekeres et al. 2015). Infections in small mammals are lifelong (Gern et

133 al. 1994; Humair et al. 1999). Transovarial transmission is assumed to be null or rare (Rollend et al.  
134 2013).

135 Here, we investigated at a local scale how landscape composition, configuration, and resulting habitat  
136 connectivity for small mammals, directly or *via* relationships with species abundances, can explain the  
137 prevalence of *A. phagocytophilum* and *B. burgdorferi* s.l. in small mammals. We specifically tested  
138 the three following hypothesis on the prevalence drivers:

139         **(H1)** Host population size: prevalence would be higher in sites supporting larger host  
140 populations (i.e. in wooded habitat patches either of large area, with more surrounding wooded  
141 habitats and/or more connected).

142         **(H2)** Overall host community competence: the landscape would indirectly influence the  
143 prevalence by acting on the relative abundance of host species exhibiting different reservoir  
144 competence, modifying the overall community competence.

145         **(H3)** Infectious agents' specificity: a stronger relationship between the prevalence and  
146 landscape variables would be observed for the *A. phagocytophilum* ecotype specific to small  
147 mammals, than for the *B. burgdorferi* s.l. group, which shows a wider range of host and of vector  
148 species.

149

## 150 **Materials and Methods**

### 151 ***Study area***

152 The study took place in the 'Zone Atelier Armorique' (Brittany, France), a 132 km<sup>2</sup> Long-Term  
153 Ecological Research (LTER) area labeled by the CNRS (Centre National de la Recherche Scientifique)  
154 and belonging to the International LTER network. This area includes different landscapes with various  
155 land uses, from deciduous mixed forest, to livestock-crop mixed farming landscapes, to cereal-  
156 oriented (mainly cereals and maize) open farming landscapes. Compared to mixed farming landscapes,  
157 open farming landscapes have fewer (and smaller) woodlots (area: 10% vs 15%), fewer grasslands  
158 (area: 20% vs. 40%), larger crops patches (mean area: 2.3 ha vs. 1.3 ha), and looser hedgerow  
159 networks (50 vs. 115 m/ha) (Millán de la Peña et al. 2003; Al Hassan et al. 2012; Perez et al. 2016).

160

### 161 ***Sampling strategy***

162 Wooded habitats support higher abundances of small mammals, better abiotic conditions for ticks  
163 (moisture) and are as such supposed to be key habitats for small mammals-ticks interactions (Boyard  
164 et al. 2008). For these reasons, 24 sampling sites were selected in wooded habitat patches in various  
165 landscape contexts (Perez et al. 2016). The 24 sampling sites, at least 500 m apart from each other to  
166 ensure their spatial independence, were placed as follows: six in the forest core; six in forest edge

167 landscapes; six in mixed farming landscapes; and six in open farming landscapes. In each of the two  
168 agricultural landscape types, three sites were selected along hedgerows (six sites overall) and three  
169 along woodlots edges (six sites overall). At forest edges and in agricultural landscapes, the sampling  
170 sites (n = 18) were selected at the ecotones between wooded habitats and grasslands, as meadows are  
171 less unfavorable to ticks than cultivated plots. Because small mammals start breeding in spring and  
172 populations peak generally in autumn, we sampled in May-June and in October in 2012 and 2013.  
173 These periods of the year also correspond to the main and the secondary activity peak of *I. ricinus*  
174 nymphs, respectively, and conversely for *I. trianguliceps* adult females, while the nymphs of this latter  
175 species are active from summer to mid-autumn (Randolph 1975a).

176

### 177 ***Small mammal sampling and ethic statement***

178 Small mammals were trapped using French model (INRA) live traps with wooden dormitory boxes.  
179 These traps can catch small mammals from 4 to 40 grams, including shrews and small rodents. Trap-  
180 lines (100 m-long) were constituted of 34 traps (three meters apart) baited with a mix of commercial  
181 seeds for pet rodents (sunflower, wheat, etc.), dry cat food, and a piece of apple for water supply.  
182 Traps were checked in the morning after 24 and 48 hours. Animals were brought to the field lab to be  
183 identified at the species level, euthanized by pentobarbital injection, weighted, sexed and dissected.  
184 Traps were designed to limit as much as possible the stress or injury of the animals. The bait was  
185 designed to obtain an optimal catch rate across small mammal species and a good survival of  
186 individuals. Targeted animals were not protected species and thus no special authorization was needed,  
187 according to the French law in force. All individuals were euthanized by authorized experimenters  
188 according to current French law and to the European guidelines on the use of animals in science  
189 (Close et al. 1997).

190

### 191 ***Molecular detection of infectious agents***

192 DNA was extracted from small mammal spleens and ears with Macherey-Nagel NucleoSpin Tissue  
193 kits (Chastagner et al. 2016). The screening for *A. phagocytophilum* was performed on DNA extracts  
194 from small mammal spleens by real-time PCR targeting the *msp2* genes according to the protocol of  
195 Courtney et al. (2004). The screening for *B. burgdorferi* s.l. was performed on DNA extracts from  
196 small mammal ears by real-time PCR in SybrGreen according to the protocol of Halos et al. (Halos et  
197 al. 2010). The *B. burgdorferi* s.l. prevalence was low and, for technical reasons, identifying them to  
198 the geno-species level (genetically discriminated *Borrelia* species) was not possible (data not shown).  
199 Thus, all the *B. burgdorferi* s.l. genospecies were combined hereafter. Although all geno-species  
200 which can infect small mammals do not share the same host range, *B. afzelii* is known to be  
201 predominant in the captured species (Kurtenbach et al. 2002a; Marsot et al. 2013). Therefore, this

202 simplification is assumed not to bias results. As temporal the variation of prevalence has been studied  
203 elsewhere (Perez et al. 2017), the data from all the sampling sessions were grouped for each site to  
204 study only the spatial variation hereafter.

205

## 206 *Landscape variables*

### 207 *Landscape data*

208 The used landscape data were: a shapefile of the land cover of 2012 kindly provided by the 'LETG-  
209 COSTEL-Rennes' lab *via* the 'Zone Atelier Armorique'; a road network shapefile provided by the  
210 'Institut National de l'Information Géographique et Forestière' (IGN); and a 5 m-resolution raster file  
211 of the land cover of 2010 from Gil Tena et al. (2014) for woodland and hedgerows. The land covers  
212 were characterized as "woodland", "hedgerows" (abandoned lands and hedgerows extracted from the  
213 5 m-resolution raster file), "grassland", "crops", "roads" (ranked according to the IGN's 'road  
214 importance index'), "buildings" and "water areas". All files were aggregated with ArcGIS 10.3.1 for  
215 Desktop, Esri ©, into a single 5 m-resolution raster file that was used in subsequent analyses.

216

### 217 *Landscape composition and configuration variables*

218 The proportion of wooded habitats ('Wooded' hereafter), computed as the proportion of  
219 "woodland"/"hedgerows" pixels, was chosen as a landscape composition variable representative of the  
220 amount of favorable permanent habitats surrounding trap-lines. The proportion of wooded ecotones  
221 surrounding trap-lines ('Ecotones' hereafter), computed as the proportion of 'wooded habitat' and  
222 "grassland"/"crops"/"roads" adjacent pixels (pixel couples), was chosen as a landscape configuration  
223 variable. Such ecotones are known to be favorable to generalist species and are places where species  
224 from different habitat can co-occur (Meunier et al. 1999; Ouin et al. 2000; Boyard et al. 2008). This  
225 configuration variable depends on landscape heterogeneity, and is maximal in landscapes with  
226 moderate woodland fragmentation.

227 The relationships between landscape variables and small mammal abundances or infection prevalence  
228 were evaluated at various spatial scales by computing these variables in circular zones of various radii  
229 around trap-line centres with Chloé2012 software (Boussard and Baudry 2014). Because trap-lines  
230 were 100 m-long, the first circular 50 m-radius zones were considered as informative on trapping  
231 habitats only ('local'). Larger circular zones with an additional 50, 100, 200, and 500 m radius were  
232 considered.

233

### 234 *Landscape habitat connectivity metrics*

235 The dispersal of the studied infectious agents is known to rely mostly on larval ticks, which acquire  
236 them by feeding on an infected small mammal and falling off in the latter's home range. The dispersal  
237 of infectious agents by young small mammals, which have not yet been highly exposed to ticks and  
238 are thus yet unlikely infected, can be considered as negligible (Randolph 1975b; Sinski et al. 2006;  
239 Kallio et al. 2014; Perez et al. 2017). Furthermore, despite *I. ricinus* nymphs can disperse bacteria on  
240 longer distances attached on hosts with larger home ranges, small mammals are unlikely to be infected  
241 by *I. ricinus* adult females because they rarely host them. For these reasons, we performed the  
242 functional connectivity analysis at the scale of small mammals' home ranges.

243 Thus, we modelled the functional connectivity of the landscape for small mammals to evaluate its  
244 relationship with their infection prevalence. We used the difference in Probability of Connectivity  
245 metric ('dPC'), which is an integrative measure of reachable habitats based on a negative exponential  
246 function (Saura and Pascual-Hortal 2007). The three dPC fractions were also used separately: the  
247 intra-patch connectivity ('dPCintra'; no inter-patch displacement/dispersal), which is dependent of  
248 patch area only, so this latter variable was used instead for simplification purpose ('Area'); the inter-  
249 patch connectivity ('dPCflux') and the "stepping stone" connectivity ('dPCconnector'; connecting  
250 other patches).

251 Land cover cost files were built only for the two dominant rodent species with contrasted habitat  
252 preference: wood mice and bank voles (Boyard et al. 2008). Because these species move preferentially  
253 along linear structures or across the shortest path between suitable habitat patches (Zhang and Usher  
254 1991), the functional distance between two habitat patches was set using least cost path distances. For  
255 "woodland", "grassland" and "crops", costs were assigned like the inverse of the relative species  
256 abundance from the literature (Ouin et al. 2000; Tattersall et al. 2002; Boyard et al. 2008; Vourc'h et  
257 al. 2008). The reference cost for "woodland" was one. For wood mice and bank voles, the chosen  
258 costs were respectively four and fifteen for "grassland", and five and fifteen for "crops". A maximum  
259 cost of 100 was assigned arbitrary to "water areas" and "buildings". Roads are repulsive habitats for  
260 small mammals because they impede their displacements (Mader 1984; Rico et al. 2007). They also  
261 cause a traffic-related mortality (Ruiz-Capillas et al. 2015). Eskildsen (2010) reported that finding  
262 bank voles were 15 times less likely on the opposite side of a barrier (forest path or road) than on the  
263 same side. Thus, a gradient of costs from 15 (countryside and forest tracks) to 75 (expressways) was  
264 assigned to "roads" according to the 'road importance index'.

265 The median distance travelled by an individual was modelled using negative exponential functions  
266 based on data from the same landscapes (Papillon et al. 2002), and from a forest landscape of the  
267 Berkshire, United-Kingdom (Kikkawa 1964). In consistency with the lower mobility of bank voles  
268 compared to wood mice, these distances were estimated at 25 and 100 m, respectively (Zhang and  
269 Usher 1991). The nodes were defined as patches with an area of at least 0.025 ha, corresponding to the  
270 minimum home range size of the studied species (Kikkawa 1964). Graphs were created based on least

271 cost path networks for each species. To compute connectivity measures with ‘isolation by distance’  
272 models, graphs based on Euclidian distance were also created for displacement/dispersal distances  
273 corresponding to half the radius used to compute land cover variables: 25, 50, 100, and 250 m. Nodes  
274 were adjacent woodland habitats pixels (“woodland” and “hedgerows”).

275 Connectivity measures were computed at the patch level for each graph. Because habitat patch areas  
276 and ‘dPC’ values were over-dispersed, those variables were log-transformed hereafter. Least cost  
277 paths, graphs, and connectivity measures were computed using Graphab 1.2.3 (Foltête et al. 2012). An  
278 example of resulting graphs is shown in **Appendix 1**. A summary of all the landscape variables is  
279 shown in **Table 1**.

280

### 281 *Data analyses*

282 To determine whether prevalence in wood mice and bank voles should be modelled separately, we  
283 first tested, for each infection, the correlation between prevalence in each species and the correlation  
284 between numbers of infected individuals of each species. Because of the non-normal distribution of  
285 prevalence data (Shapiro-Wilk test:  $p < 0.05$ ), we used Spearman’s correlation tests.

286 To assess indirect effects of landscape structure on prevalence *via* the abundances of small mammal  
287 species, the relationship between these latter and landscape variables was tested. First, to determine  
288 whether wood mouse and bank vole abundances could be modelled separately, their correlation was  
289 tested through Pearson’s correlation test. Then, to choose the most appropriate error distribution of  
290 species abundances, Akaike Information Criterion corrected for finite sample size (AICc; Hurvich and  
291 Tsai 1989) values of the null models fitted with a normal error distribution and with a Poisson error  
292 distribution were compared. The normal error distribution had a better support (lower AICc-value) for  
293 wood mouse abundance (AICc-normal = 180.2, AICc-Poisson = 232.0) and for bank vole abundance  
294 (AICc-normal = 141.6, AICc-Poisson = 154.9). Species abundances were thus modelled using Linear  
295 Models (LMs).

296 The variables were first selected in single explanatory variable models ( $p < 0.1$ ). Then, multiple  
297 explanatory variable LMs were built with the selected variables. To avoid collinearity problems,  
298 models with correlated variables ( $|r| > 0.5$ ) were excluded. The models were then ranked based on  
299 AICc values, and the significance of the variable in the best models ( $\Delta AICc < 2$ ) was evaluated with  
300 type II ANOVAs ( $p < 0.05$ ).

301 To assess whether prevalence were related to landscapes variables or species abundances, prevalence  
302 in small mammals per site was modelled using binomial Generalized Linear Models (GLMs) with the  
303 same explanatory landscape variables as above, with addition of wood mouse abundance (N.As), bank  
304 vole abundance (N.Mg), and the ratio between the bank vole abundance and the wood mouse  
305 abundance (ratio.Mg:As). Abundances were expressed as the total number of captured individuals per

306 site. The variables were first selected in single explanatory variable models ( $p < 0.1$ ). Another AICc-  
307 based model ranking and variable significance evaluation was finally performed on multiple  
308 explanatory variable GLMs, as described above.

309 All statistical analyses were performed using R software Version 1.2.5001 (R Development Core  
310 Team 2019). The R-package 'car' was used for ANOVAs, 'MuMIn' for model selections, and 'psych'  
311 for pairwise correlation tests between explanatory variables. The absence of autocorrelation in the  
312 dependent variables was checked using the 'correlog' function of the 'nfc' R-package.

313

## 314 **Results**

315 A total of 612 small mammals belonging to five species were caught during the two sampling years  
316 (see **Table 2** for detailed results; the whole data set is available in supplementary material). Wood  
317 mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) were largely dominant (74.2% and  
318 24.3% of captured animals, respectively) and found in all the 24 sites. We captured nine individuals of  
319 three other species on seven sites: four field voles (*Microtus agrestis*) on three sites, two common pine  
320 voles (*Microtus subterraneus*) on two sites, and three crowned shrews (*Sorex coronatus*) on three  
321 sites. A maximum of four species were present in a single forest core site with all species excepting  
322 the common pine vole.

323 Wood mouse abundance and bank vole abundance were not correlated ( $\rho = 0.229$ ,  $p = 0.281$ ) and  
324 thus have been analysed separately hereafter. The best model for wood mouse abundance included  
325 only the proportion of ecotones in 500 m-radius zones ( $R^2 = 0.290$ ,  $p = 0.003$ ) with a positive  
326 relationship. Bank vole abundance was not significantly related to any landscape variable ( $p > 0.05$ ).

327

### 328 *Results for A. phagocytophilum*

329 The analyses of *A. phagocytophilum* prevalence were based on the PCR results for 452 wood mice,  
330 147 bank voles, four field voles, two common pine voles and three crowned shrews. Twenty wood  
331 mice, twenty bank voles and two crowned shrews were positive (**Table 2**). The number of positive  
332 wood mice and bank voles per site were significantly correlated ( $\rho = 0.425$ ,  $p = 0.038$ ). However,  
333 the prevalence were not ( $\rho = 0.291$ ,  $p = 0.177$ ). The results of the selection procedure of the GLMs  
334 of *A. phagocytophilum* prevalence as a function of landscape variables and species abundance  
335 variables are detailed in **Table 3**.

336 The most supported GLM of *A. phagocytophilum* prevalence in all small mammals included bank vole  
337 abundance, (**Figure 1a**), and the proportion of wooded habitats in 50 m-radius zones, both displaying  
338 a significant positive relationship with the prevalence (**Figure 1a** and **1b**, respectively). The most  
339 supported GLM of prevalence in wood mice included bank vole abundance and the proportion of

340 wooded habitats in the trapping habitats, both displaying a significant positive relationship (**Figure 1c**  
341 and **1d**). The ratio between bank vole and wood mouse abundances was significantly positively related  
342 to the prevalence in wood mice in the univariate model (not shown). The most supported GLM of  
343 prevalence in bank voles included the bank vole abundance, the proportion of wooded habitats in  
344 50 m-radius zones, and the proportion of ecotones in 200 m-radius zones, all displaying a significant  
345 positive relationships with the prevalence (**Figure 1e, 1f, and 1g**, respectively). The relationship  
346 between prevalence and ecotones was negative in single explanatory variable models considering all  
347 sites, but positive when excluding forest sites (not shown). Thus, the apparent contradiction between  
348 single and multiple explanatory variables models likely results from the reduction of ecotones length  
349 in highly wooded landscapes (see the prevalence as a function of both landscape variables in  
350 **Figure 1h**).

351

#### 352 *Results for B. burgdorferi s.l.*

353 The analyses of *B. burgdorferi s.l.* prevalence were based on the PCR results for 450 wood mice, 147  
354 bank voles, four field voles, two common pine voles and three crowned shrews. Fifteen wood mice,  
355 ten bank voles and one common pine vole were positive (**Table 2**). The numbers of positive wood  
356 mice and bank voles per site were not significantly correlated neither was the prevalence ( $p > 0.05$ ).  
357 The results of the selection procedure of the GLMs of *B. burgdorferi s.l.* prevalence as a function of  
358 landscape variables and species abundance variables are detailed in **Table 4**.

359 For all small mammals, the only significant variable in GLMs of *B. burgdorferi s.l.* prevalence  
360 included the proportion of ecotones in 50 m-radius zones, displaying a significant positive relationship  
361 (**Figure 2a**). For prevalence in wood mice separately, no landscape variable displayed a significant  
362 relationship. The most supported GLM of prevalence in bank voles included only the proportion of  
363 ecotones in 100 m-radius zones, displaying a significant positive relationship (**Figure 2b**). This  
364 variable computed in the trapping habitats was also significant. The proportion of wooded habitats in  
365 the trapping habitats and in 50 m-radius zones displayed a significant negative relationship (not  
366 shown). No species abundances variable was significantly related to any prevalence.

367

#### 368 **Discussion**

369 In this study, we investigated the possible associations between landscape structure, abundances of  
370 small mammal species and the prevalence of two tick-borne infectious agents in small mammals, to  
371 better understand the spread of these infectious agents in the landscape. The small mammal  
372 community at the woodland/hedgerows-grassland ecotones and in forest sites was dominated by the  
373 wood mouse and the bank vole, two rodent species with different habitats use, and as such interesting  
374 to compare at this landscape scale. However, we found only that the wood mouse abundance was

375 positively correlated to the proportion of ecotones in 500 m-radius zones. This finding is consistent  
376 with the propensity of this generalist species to use various complementary habitats (Tew and  
377 Macdonald 1994; Ouin et al. 2000). Despite bank vole abundance was not associated to any landscape  
378 variable here, in a previous study considering seasonal variation, negative associations with two  
379 landscape structural connectivity variables was observed in spring (Perez et al. 2016). Such  
380 relationships, also reported in several other studies, are likely caused by a released predation pressure  
381 in fragmented landscapes (Szacki 1987; van Apeldoorn et al. 1992; Paillat and Butet 1996; Michel et  
382 al. 2007).

383

#### 384 *Prevalence of Anaplasma phagocytophilum*

385 The numbers of positive individuals as well as the prevalence in wood mice and bank voles were  
386 correlated, suggesting a common infection factor and/or an increased exposition of one species in the  
387 presence of the other. We observed a higher prevalence in bank voles and a positive, despite weak,  
388 relationship between bank vole abundance and the prevalence in all small mammals and in species  
389 separately. Although not related to landscape variables, these results support an effect of relative host  
390 species abundances on prevalence (**H2**): bank vole likely acts as an amplification host species for the  
391 transmission of these bacteria, while wood mouse acts, comparatively, rather as a dilution host species  
392 (Rosso et al. 2017; Perez et al. 2017).

393 Several studies demonstrated that the prevalence of directly transmitted infectious agents increased  
394 with host population size, and decreased with population isolation as a consequence of a higher local  
395 extinction risk (Begon et al. 2003; Guivier et al. 2011). Here, the proportion of wooded habitats in the  
396 surrounding landscape was positively associated to *A. phagocytophilum* prevalence in all small  
397 mammals and in species separately. More wooded landscapes probably support larger and more  
398 connected populations of bank voles resulting in a lower local extinction probability in a given habitat  
399 patch (Paillat and Butet 1996). Consequently, a lower local extinction probability of their parasites  
400 (including small mammal specialist tick species like *I. trianguliceps* and *I. acuminatus*), and of the  
401 infectious agents they could transmit is expected (**H1**).

402

#### 403 *Prevalence of Borrelia burgdorferi sensu lato*

404 The *B. burgdorferi* s.l. prevalence in small mammals, particularly in bank voles, was positively related  
405 to the proportion of ecotones within 100 m. These results suggest an enhanced transmission of these  
406 bacteria at the interface between wooded and open (crops and grassland) habitats and therefore in  
407 fragmented landscapes where such ecotones are frequent. A possible explanation of increased  
408 *B. burgdorferi* s.l. prevalence in such landscapes is an increased density of small mammals and other  
409 hosts, causing an increased density of *I. ricinus* nymphs, resulting in an amplification of the

410 transmission cycle (Agoulon et al. 2012; Li et al. 2012; Cayol et al. 2018). However, in previous  
411 studies, no relationship was observed between the abundance of *I. ricinus* nymphs and  
412 *B. burgdorferi* s.l. prevalence, and tick density was generally higher in woodlands (Boyard et al. 2008;  
413 Hoch et al. 2010; Perez et al. 2017). An alternative explanation is an increased density of hosts  
414 competent for the same geno-species than small mammals (Vourc'h et al. 2008).

415 The mobility of the wood mouse and its ability to use crops and grassland could explain the absence of  
416 spatial pattern in the *B. burgdorferi* s.l. prevalence of this species. Several studies showed that wood  
417 mice, more prone to host *Ixodes* sp. larvae than bank voles, may yield more nymphs infected by those  
418 bacteria despite displaying lower bacterial loads (Humair et al. 1993, 1999). Thus, wood mice might  
419 act as medium distance dispersers (at least up to 500 m) of infected *Ixodes* sp. larvae that become  
420 infective nymphs, as previously suggested in other studies (Boyard et al. 2008; Gassner et al. 2008).  
421 These results support the role of host specificity of infectious agents on their distribution patterns  
422 (**H3**).

423 For both infections, prevalence models were not improved by using wooded habitats connectivity  
424 measures compared to simpler landscape variables. In our study area, variations in wooded habitats  
425 connectivity were maybe not contrasted enough to be captured (Michel et al. 2007). Alternatively,  
426 within each considered land cover, the influence of habitat quality and heterogeneity on landscape  
427 connectivity for small mammals might have been overlooked and should be accounted for in higher  
428 resolution models and/or habitat quality based landscape connectivity models (Mortelliti et al. 2010).  
429 It would also be interesting to account for other potential factors affecting small mammal communities  
430 and their tick-borne infection prevalence, like predation pressure (Hofmeester et al. 2017).

431 Finally, species which were rare in the sampled habitats (crowned shrew, field vole and common pine  
432 vole) can also host *A. phagocytophilum* and/or *B. burgdorferi* s.l. (Bown et al. 2008, 2009, 2011).  
433 Further studies including habitats where these species can be more abundant (e.g. fallow lands, fields'  
434 margins, clear cuts) and focusing on more hosts species, especially for *B. burgdorferi* s.l., would allow  
435 a better overall view of the distribution and the spread of these infectious agents in the landscape.

436

### 437 *Conclusion*

438 The *A. phagocytophilum* prevalence could be substantially explained by a positive association with the  
439 proportion of wooded habitats in the surrounding landscape at least up to 500 m, validating the host  
440 population size hypothesis (**H1**). The *B. burgdorferi* s.l. prevalence could be explained only by the  
441 presence of ecotones within 100 m. Despite a weak positive relationship between bank vole abundance  
442 and *A. phagocytophilum* prevalence, no indirect effect of landscape variables on this prevalence has  
443 been detected, questioning the overall host community competence hypothesis (**H2**). Indeed, only  
444 wood mice abundance was significantly linked to our landscape variables, but at larger scales than the

445 relationships between landscape variables and the prevalence. The prevalence of the two infections  
446 displayed contrasted spatial patterns, a difference which likely results from the wider range of hosts  
447 and vectors of *B. burgdorferi* s.l., as predicted by the infectious agent specificity hypothesis (**H3**). As a  
448 whole, our results demonstrate the interest of integrating complementary approaches, such as  
449 landscape ecology and community ecology, to better understand the dynamics and the spatial  
450 distribution of tick-borne infectious agents to prevent epidemiological risks at the scale of agricultural  
451 landscapes.

452

### 453 **Competing interests**

454 The authors declare no competing interests

455

### 456 **Authors' contributions**

457 GP, SB, AA, GV, OP and AB designed the study. GP, SB, AA, YR, OP and AB participated to the  
458 small mammal field sampling. AC performed most of the DNA extractions and the molecular  
459 analyses. YR managed the GIS data. GP performed all data analyses and drafted the manuscript. All  
460 authors read, commented and approved the manuscript.

461

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477

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**Table 1: Landscape variables used in the study for the model selection procedures.**

Variable	Scale (m) <sup>a</sup>	Unit	Mean	Median	Range (min; max)
Proportion of wooded habitats					
Wooded.local	0	Proportion of pixels	0.569	0.557	0.051; 1.000
Wooded.50m	50	Proportion of pixels	0.511	0.495	0.053; 0.986
Wooded.100m	100	Proportion of pixels	0.487	0.441	0.039; 0.988
Wooded.200m	200	Proportion of pixels	0.453	0.352	0.042; 0.990
Wooded.500m	500	Proportion of pixels	0.420	0.3	0.034; 0.970
Proportion of ecotones					
Ecotones.local	0	Proportion of pixel couples	0.058	0.051	0.000; 0.132
Ecotones.50m	50	Proportion of pixel couples	0.048	0.042	0.021; 0.090
Ecotones.100m	100	Proportion of pixel couples	0.042	0.041	0.017; 0.075
Ecotones.200m	200	Proportion of pixel couples	0.034	0.030	0.014; 0.057
Ecotones.500m	500	Proportion of pixel couples	0.027	0.027	0.012; 0.047
Connectivity measures					
log(Area)	Patch	m <sup>2</sup>	11.15	11.14	6.48; 14.57
log(dPC.Euclidian.25m)	25	none	6.17	5.36	-2.00; 12.73
log(dPC.Euclidian.50m)	50	none	6.26	5.16	-2.08; 12.73
log(dPC.Euclidian.100m)	100	none	6.35	5.08	-2.12; 12.71
log(dPC.Euclidian.250m)	250	none	6.62	5.42	-1.82; 12.72
log(dPC.lcp.As.100m) <sup>b</sup>	100	none	6.52	5.61	-2.01; 12.79
log(dPC.lcp.Mg.25m) <sup>c</sup>	25	none	5.99	5.84	-3.20; 12.76
log(dPCflux.Euclidian.25m)	25	none	5.09	3.61	-3.09; 12.26
log(dPCflux.Euclidian.50m)	50	none	5.51	3.96	-2.63; 12.43
log(dPCflux.Euclidian.100m)	100	none	5.77	4.12	-2.57; 12.49
log(dPCflux.Euclidian.250m)	250	none	6.22	4.77	-2.05; 12.49
log(dPCflux.lcp.As.100m) <sup>b</sup>	100	none	5.63	4.17	-2.81; 12.29
log(dPCflux.lcp.Mg.25m) <sup>c</sup>	25	none	2.03	1.36	-10.78; 10.21
log(dPCconnector.Euclidian.25m+1)	25	none	0.62	0.0000	0.000; 3.89
log(dPCconnector.Euclidian.50m+1)	50	none	1.56	0.0000	0.000; 7.17
log(dPCconnector.Euclidian.100m+1)	100	none	2.08	0.0121	0.000; 9.22
log(dPCconnector.Euclidian.250m+1)	250	none	2.78	0.2520	0.000; 10.35
log(dPCconnector.lcp.As.100m+1) <sup>b</sup>	100	none	1.04	0.0801	0.000; 7.98
log(dPCconnector.lcp.Mg.25m+1) <sup>c</sup>	25	none	5.79 <sup>e-3</sup>	0.0000	0.000; 0.109

<sup>a</sup> Radius of computing zones (proportions) or median movement distances (connectivity).

<sup>b</sup> As: with the friction coefficients set for *Apodemus sylvaticus*.

<sup>c</sup> Mg: with the friction coefficients set for *Myodes glareolus*.

**Table 2: Results of *Anaplasma phagocytophilum* and *Borrelia burgdorferi* s.l. PCR detection per site over the two-year sampling (2012-2013).**

Site	Landscape context <sup>a</sup>	Tested and positive individuals for <i>A. phagocytophilum</i> (Aph) and <i>B. burgdorferi</i> s.l. (Bb sl) <sup>b</sup>																			
		Asyl			Mgla			Magr			Msub			Scor			Total				
		Nbr <sup>c</sup>	Aph	Bb sl	Nbr <sup>c</sup>	Aph	Bb sl	Nbr <sup>c</sup>	Aph	Bb sl	Nbr <sup>c</sup>	Aph	Bb sl	Nbr <sup>c</sup>	Aph	Bb sl	Nbr <sup>c</sup>	Aph	Bb sl		
1	FC	11	1	0	2	0	0												13	1	0
2	FC	9	0	0	10	1	0												19	1	0
3	FC	9	0	0	2	1	0												11	1	0
4	FC	19	2	1	11	9	0	2	0	0			1	1	0				33	12	1
5	FC	19	2	1	10	2	1	1	0	0									30	4	2
6	FC	19 <sup>d</sup>	1	1	1	0	0												20	1	1
7	FE	18	2	0	13	1	0	1	0	0									32	3	0
8	FE	32	2	2	3	1	0												35	3	2
9	FE	20	0	0	11	1	1												31	1	1
10	FE	18	1	1	1	0	0				1	0	0						20	1	1
11	FE	2	0	0	1 <sup>d</sup>														3	0	0
12	FE	8 <sup>d</sup>	0	0	2	0	0												10	0	0
13	ME	21	2	0	6 <sup>d</sup>	0	0												27	2	0
14	ME	32	3	2	12	4	1												44	7	3
15	ME	24	0	0	7	0	1												31	0	1
16	MH	29	2	1	13	0	2												42	2	3
17	MH	21	0	0	6	0	1												27	0	1
18	MH	40 <sup>e</sup>	0	1	4	0	0				1	0	1						45	0	2
19	OE	32	0	1	4	0	0												36	0	1
20	OE	9	0	0	5	0	0												14	0	0
21	OE	17	0	2	4	0	1												21	0	3
22	OH	16	0	1	6	0	0							1	0	0			23	0	1
23	OH	23	0	1	8	0	2												31	0	3
24	OH	6	2	0	7	0	0							1	1	0			14	3	0
<b>Total</b>	<b>24</b>	<b>454</b>	<b>20</b>	<b>15</b>	<b>149</b>	<b>20</b>	<b>10</b>	<b>4</b>	<b>0</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>1</b>	<b>3</b>	<b>2</b>	<b>0</b>			<b>612</b>	<b>42</b>	<b>26</b>
<b>% of total</b>		<b>74.2</b>	<b>3.28</b>	<b>2.47</b>	<b>24.3</b>	<b>3.28</b>	<b>1.64</b>	<b>0.65</b>	<b>0</b>	<b>0</b>	<b>0.33</b>	<b>0</b>	<b>0.16</b>	<b>0.49</b>	<b>0.33</b>	<b>0</b>			<b>100</b>	<b>6.91</b>	<b>4.29</b>
<b>Prevalence (%)</b>			<b>4.42</b>	<b>3.33</b>		<b>13.6</b>	<b>6.80</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>50.0</b>		<b>66.7</b>	<b>0</b>					<b>6.91</b>	<b>4.29</b>	

<sup>a</sup> FC: forest core; FE: forest edge; ME: mixed farming at woodlot edge; MH: mixed farming along hedgerows; OE: open farming at woodlot edge; and OH: open farming along hedgerows.

<sup>b</sup> Asyl: *Apodemus sylvaticus*; Mgla: *Myodes glareolus*; Magr: *Microtus agrestis*; Msub: *M. subterraneus*; and Scor: *Sorex coronatus*.

<sup>c</sup> Total number of individuals over the two-year sampling.

<sup>d</sup> Including one individual not tested.

<sup>e</sup> Including two individuals not tested for *B. burgdorferi* s.l. only.

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**Table 3: Best binomial Generalized Linear Models of *Anaplasma phagocytophilum* prevalence as a function of landscape variables and species abundance variables according to the AICc-based selection procedure.**

All small mammals					
Model set	Rank	Variables and their significativity	AICc	$\Delta$ AICc	R <sup>2</sup>
Null model			106.9		
Landscape	1	<b>Wooded.50m***</b>	86.5		0.332
Community	1	<b>N.Mg***</b>	96.3		0.189
	2	<b>N.Mg*</b> + Ratio.Mg:As	96.6	0.33	0.223
Community and landscape	1	<b>Wooded.50m*** + N.Mg***</b>	77.7		0.498
	2	<b>Wooded.local*** + N.Mg**</b>	78.4	0.68	0.488
Wood mice ( <i>Apodemus sylvaticus</i> )					
Model set	Rank	Variables and their significativity	AICc	$\Delta$ AICc	R <sup>2</sup>
Null model			61.5		
Landscape	1	<b>Wooded.50m*</b>	59.0		0.145
	2	<b>Wooded.local*</b>	59.1	0.05	0.143
	3	Wooded.100m <sup>o</sup>	60.4	1.32	0.105
	4	Ecotones.100m <sup>o</sup>	60.4	1.32	0.105
	5	log(Area) <sup>o</sup>	60.6	1.59	0.097
Community	1	<b>Ratio.Mg:As*</b>	59.0		0.146
	2	N.Mg <sup>o</sup>	60.4	1.42	0.101
Community and landscape	1	<b>Wooded.local* + N.Mg*</b>	57.8		0.261
	2	<b>Wooded.50m* + N.Mg<sup>o</sup></b>	58.2	0.40	0.250
	3	<b>Wooded.local* + Ratio.Mg:As<sup>o</sup></b>	58.3	0.41	0.248
	4	Wooded.50m <sup>o</sup> + Ratio.Mg:As <sup>o</sup>	58.5	0.06	0.243
	5	log(Area) + <b>Ratio.Mg:As*</b>	59.5	1.07	0.225
Bank voles ( <i>Myodes glareolus</i> )					
Model set	Rank	Variables and their significativity	AICc	$\Delta$ AICc	R <sup>2</sup>
Null model			73.0		
Landscape	1	<b>Ecotones.200m* + Wooded.50m***</b>	52.1		0.477
	2	Ecotones.200m <sup>o</sup> + <b>Wooded.100m***</b>	52.9	0.87	0.461
	3	<b>Ecotones.200m* + Wooded.200m***</b>	52.9	0.89	0.461
	4	<b>Ecotones.local***</b>	53.4	1.29	0.405
	5	<b>Wooded.100m***</b>	54.0	1.94	0.393
Community	1	<b>N.Mg*</b>	70.2		0.096
Community and landscape	1	<b>Ecotones.200m** + Wooded.50m*** + N.Mg*</b>	48.3		0.600

Only models with  $\Delta$ AICc < 2 are shown. Models with connectivity variables that performed worse than models with the wooded patch area have been discarded. Significant codes are: "\*\*\*\*" when  $p \leq 0.001$ ; "\*\*\*" when  $0.001 < p \leq 0.01$ ; "\*\*" when  $0.01 < p \leq 0.05$ ; "\*" when  $0.05 < p \leq 0.1$ ; otherwise,  $0.1 < p$ . Significant variables at  $p < 0.05$  are in bold.

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**Table 4: Best binomial Generalized Linear Models of *Borrelia burgdorferi* s.l. prevalence in small mammals as a function of landscape variables and species abundance variables according to the AICc-based selection procedure.**

All small mammals					
Model set	Rank	Variables and their significativity	AICc	$\Delta$ AICc	R <sup>2</sup>
Null model			56.7		
Landscape	1	<b>Ecotones.50m*</b>	55.2	0.00	0.201
	2	Ecotones.100m <sup>o</sup>	55.4	0.25	0.188
Community	None				
Wood mice ( <i>Apodemus sylvaticus</i> )					
Model set	Rank	Variables and their significativity	AICc	$\Delta$ AICc	R <sup>2</sup>
Null model			43.0		
Landscape	None				
Community	None				
Bank voles ( <i>Myodes glareolus</i> )					
Model set	Rank	Variables and their significativity	AICc	$\Delta$ AICc	R <sup>2</sup>
Null model			35.2		
Landscape	1	<b>Ecotones.100m*</b>	33.3	0.00	0.252
	2	<b>Ecotones.local*</b>	33.6	0.30	0.235
	3	<b>Woodes.local*</b>	33.6	0.31	0.234
	4	<b>Wooded.50m*</b>	33.7	0.40	0.229
	5	dPC.250m <sup>o</sup>	34.0	0.65	0.214
	6	Ecotones.50m <sup>o</sup>	34.0	0.67	0.213
	7	dPC.25m <sup>o</sup>	34.0	0.68	0.212
	8	Wooded.100m <sup>o</sup>	34.1	0.78	0.206
	9	dPC.50m <sup>o</sup>	34.1	0.79	0.206
	10	dPC.100m <sup>o</sup>	34.1	0.81	0.205
	11	dPC.250m + Ecotones.100m	34.2	0.85	0.350
	12	dPCflux.250m <sup>o</sup>	34.2	0.86	0.202
	13	dPC.Mg <sup>o</sup>	34.3	0.94	0.197
	14	dPCconnector.250m <sup>o</sup>	34.3	0.97	0.196
	15	Ecotones.100m + Wooded.50m	34.3	1.01	0.347
	16	log(Area) <sup>o</sup>	34.3	1.02	0.193
Community	None				

Only models with  $\Delta$ AICc < 2 are shown. Models with connectivity variables that performed worse than models with the wooded patch area have been discarded. Significant codes are: "\*\*\*\*" when  $p \leq 0.001$ ; "\*\*\*" when  $0.001 < p \leq 0.01$ ; "\*\*" when  $0.01 < p \leq 0.05$ ; "\*" when  $0.05 < p \leq$ ; otherwise,  $0.1 < p$ . Significant variables at  $p < 0.05$  are in bold.

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726 **Figure 1: The *Anaplasma phagocytophilum* prevalence in small mammals as a function of**  
727 **landscape variables and species abundance variables.**

728 The *A. phagocytophilum* prevalence, expressed as the frequency of infected individuals per site, in all  
729 small mammals (**a** and **b**), in wood mice (**c** and **d**), and in bank voles (**e**, **f**, **g** and **h**). Fitted binomial  
730 regression curves, according to the best multiple explanatory variables binomial Generalized Linear  
731 Models, are shown with 95% confidence intervals (light grey, except **h**). Prevalence is shown as a  
732 function of bank vole abundance (**a**, **c**, and **e**), as a function of the proportion of wooded habitats in 50  
733 m-radius zones (**b**, **f** and **h**) or in the trapping habitats (**d**), and as a function of the proportion of  
734 ecotones in 200 m-radius zones (**g** and **h**). Disks areas are proportional to samples sizes (see Table 2).

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736 **Figure 2: The *Borrelia burgdorferi* sensu lato prevalence in small mammals as a function of**  
737 **landscape variables.**

738 The *B. burgdorferi* s.l. prevalence, expressed as the frequency of infected individuals per site, in all  
739 small mammals (**a**), and in bank voles (**b**). Fitted binomial regression curves, according to the best  
740 single explanatory variable binomial Generalized Linear Models, are shown with 95% confidence  
741 intervals (light grey). Prevalence is shown as a function of the proportion of ecotones in 50 m-radius  
742 zones (**a**) and in 100 m-radius zones (**b**). Disks areas are proportional to samples sizes (see Table 2).

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744 **Appendix 1: Example of the habitats landscape connectivity analyses.**

745 Final aggregated land cover 5 m-resolution raster file (**a**) and 'dPC' ('difference in Probability of  
746 Connectivity') metric computed on different graphs (**b**, **c**, and **d**). The sampling patch on the right  
747 (surrounded in blue) appears moderately connected with Euclidian distances (**b**), while it is weakly  
748 connected when weighted by least cost paths (**c** and **d**) because it is surrounded by a river at North and  
749 by roads on other sides (see **a**). The sampling patch on the left is moderately connected for the wood  
750 mouse (**c**) while it is weakly connected for the bank vole (**d**) because it is separated to other wooded  
751 habitat patches by large grassland or crops patches resulting in fewer connections for this latter  
752 species. See **Materials and Methods** for more details.

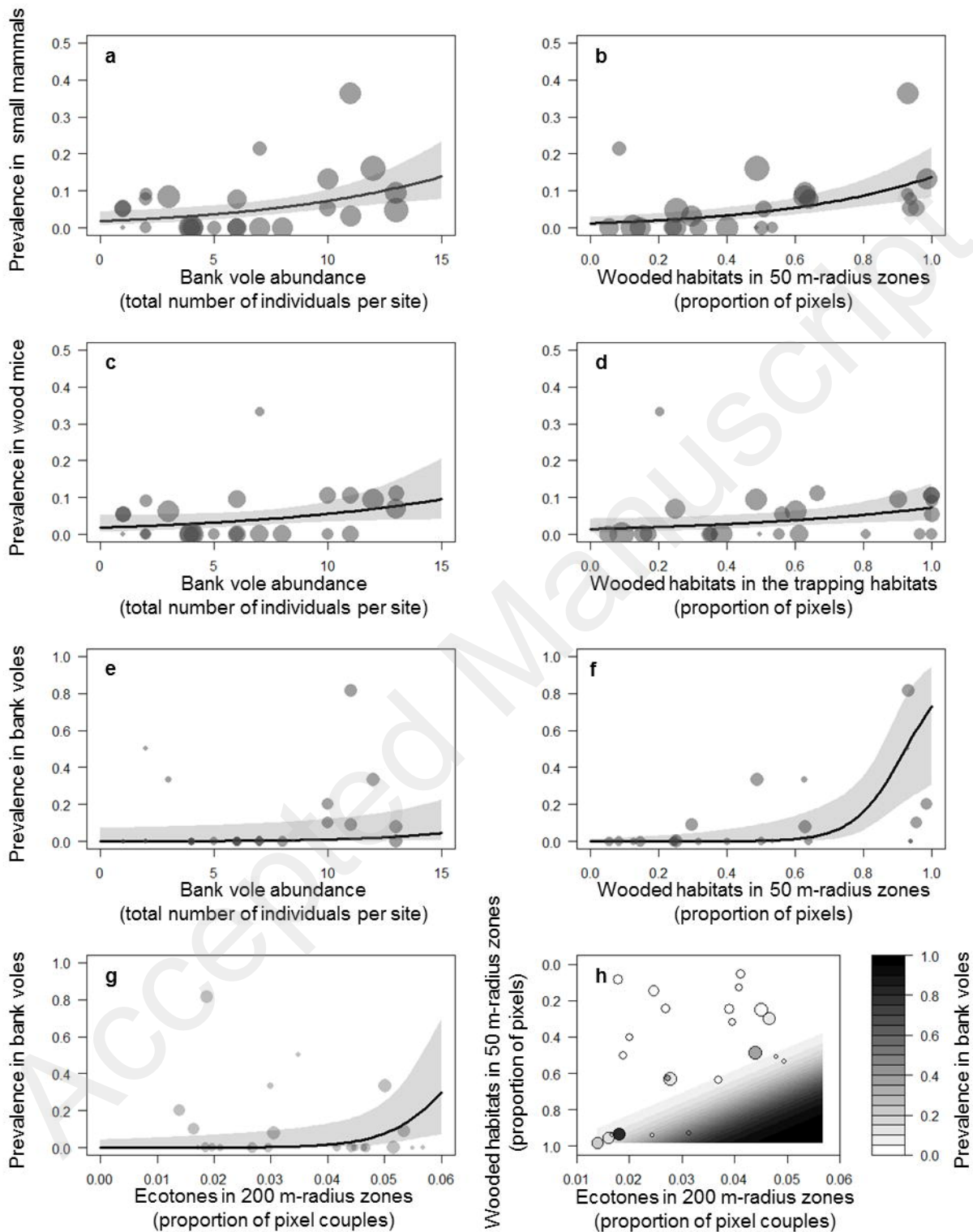


Figure 1

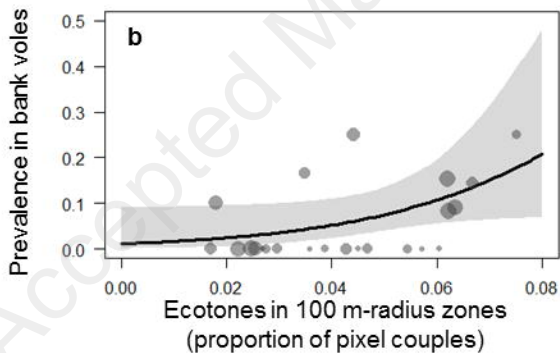
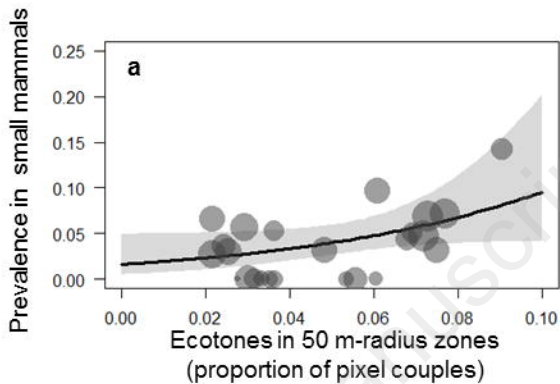


Figure 2

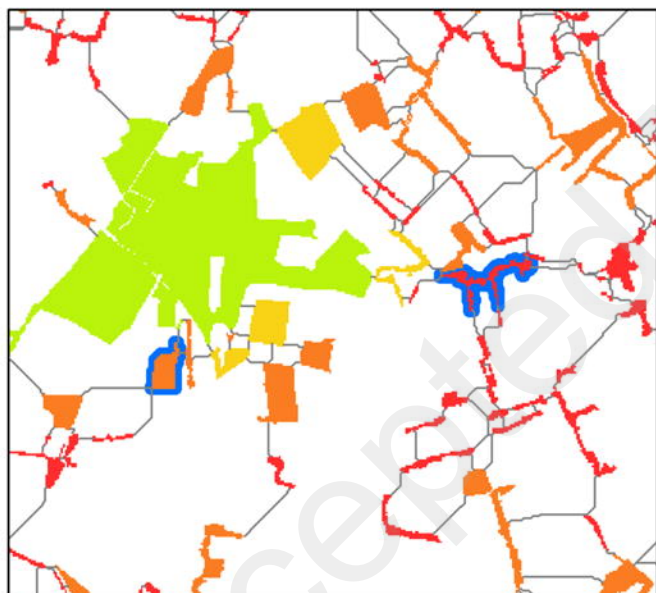
**a: Aggregated 5 m-resolution land cover raster**



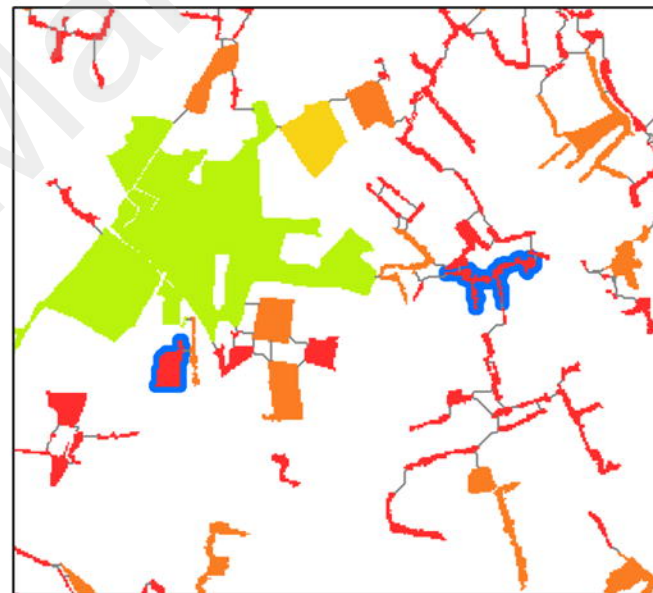
**b: Patches' connectivity (dPC) based on Euclidian distances (250 m)**



**c: Least cost paths and patches' connectivity (dPC) for the Wood mouse**

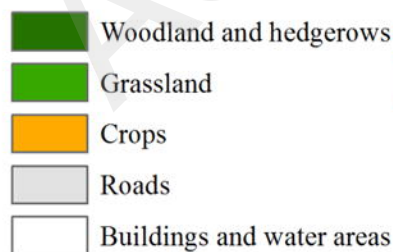


**d: Least cost paths and patches' connectivity (dPC) for the Bank vole**

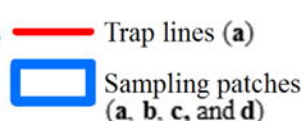


**Legend**

**Land covers for a.**



**Sampling sites**



**Connectivity measures (dPC) for b, c and d.**

