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**The distribution, phenology, host range and
pathogen prevalence of *Ixodes ricinus* in France:
a systematic map and narrative review**

Grégoire Perez^{1,2,3,*}, Laure Bournez⁴, Nathalie Boulanger^{5,6}, Johanna Fite⁷, Barbara Livoreil⁸, Karen D. McCoy⁹,
Elsa Quillery⁷, Magalie René-Martellet^{10,11}, and Sarah I. Bonnet^{12,13}

¹ UMR 0956 BIPAR, Ecole nationale vétérinaire d'Alfort – ANSES – INRAE, 94701 Maisons-Alfort, France

² UMR 5558 LBBE, université Claude Bernard Lyon 1 – VetAgro Sup – CNRS, 69622 Villeurbanne, France

³ Laboratoire Cogitamus

⁴ Laboratoire de la rage et de la faune sauvage de Nancy, ANSES, 54220 Malzéville, France

⁵ UR 7290 Virulence bactérienne précoce, FMTS, Université de Strasbourg, 67000 Strasbourg, France

⁶ Centre National de Référence Borrelia, Centre Hospitalier Universitaire, 67000 Strasbourg, France

⁷ Direction de l'Évaluation des Risques, ANSES, 94701 Maisons-Alfort, France

⁸ Evidence synthesis consultant, Collaboration for Environmental Evidence France, 83340 Le Luc en Provence, France

⁹ UMR MiVEGEC, CNRS – IRD – Université de Montpellier, 34394 Montpellier, France

¹⁰ UMR EPIA, Université de Lyon – INRAE – VetAgro Sup, 69280 Marcy l'Etoile, France

¹¹ UMR EPIA, Université Clermont Auvergne – INRAE – VetAgro Sup, 63122 Saint-Genès-Champanelle, France

¹² INRAE, Animal Health Department, 37380 Nouzilly, France

¹³ UMR 2000 Ecology and Emergence of Arthropod-borne Pathogens unit, Institut Pasteur – CNRS – Université Paris-Cité, 75015 Paris, France.

* Corresponding author: perez.gregoire@gmail.com, Orcid ID: 0000-0001-8861-4856

Current affiliation: UMR ASTRE, CIRAD – INRAE, Campus de Baillarguet, 34980 Montferrier-sur-Lez, France

26 **Abstract:**

27 The tick *Ixodes ricinus* is the most important vector species of infectious diseases in European France.
28 Understanding its distribution, phenology, and host species use, along with the distribution and prevalence of
29 associated pathogens at national scales is essential for developing prevention strategies. The aim of this paper
30 is to provide a systematic map and narrative review of the existing knowledge on the eco-epidemiology of
31 *I. ricinus* in France. Using literature published up to 2020, the present paper provides a distribution map for the
32 species and a summary of environmental factors explaining observed geographical differences in phenology and
33 temporal differences in abundance. The diversity of vertebrate host species used by this tick, along with their
34 degree of infestation when available, are presented and discussed with respect to their potential contribution to
35 the population dynamics of *I. ricinus* and the circulation of tick-borne zoonotic pathogens. Prevalence data of
36 detected pathogens are summarised in different maps. Results from 187 identified references show that the
37 species is present in most departments, but scarce under Mediterranean climate and in coastal habitats. Its
38 phenology is generally bimodal with variations depending on climate. Abundance seems positively influenced by
39 forest cover and host abundance. Rodents and ruminants are the most studied species groups, but the diversity
40 of sampling protocols (e.g., location, season, exhaustivity of inspection) precluded direct comparisons between
41 species groups. Data on pathogens are patchy, with most studies conducted near research units. Among
42 pathogens, *Borrelia burgdorferi* sensu lato is the most searched for in ticks and seems more prevalent in north-
43 eastern and central France. The review carried out here has made it possible to highlight the gaps in our
44 knowledge of tick-host-pathogen interactions, their ecology and their distribution, and the need to address these
45 gaps in order to optimize tick and tick-borne diseases prevention and control strategies.

46

47 **Keywords:** *Anaplasma*; *Babesia*; *Bartonella*; *Borrelia*; *Coxiella*; *Francisella*; *Theileria*; *Rickettsia*; tick-borne
48 encephalitis virus; hard tick; tick-borne diseases.

49 **1 Introduction**

50 Among the forty one tick species known to be present in European (metropolitan) France (i.e., excluding the
51 ultra-marine French territories, France hereafter), the hard tick *Ixodes ricinus* is the most frequently involved in
52 human tick bites (Gilot & Marjolet 1982; Pérez-Eid 2007). This tick transmits several pathogens responsible for
53 human and animal diseases (e.g. Lyme borreliosis, tick-borne encephalitis, piroplasmosis, anaplasmosis)
54 (Heyman et al. 2010). Both the biology and ecology of this European tick species have been recently reviewed
55 by Gray et al. (2021), and are known to vary greatly among regions. Data collected at national levels can provide
56 insight into the factors responsible for at least some of this variation, but are rarely available to the scientific
57 community because of a mix of published and unpublished work and its production in different languages. Here,
58 we synthesize the available data on *I. ricinus* and its associated pathogens in France up to 2020.

59 Some aspects concerning the life cycle of *I. ricinus* are well-known. For example, like most hard ticks (*Ixodidae*),
60 each life stage of *I. ricinus* (larva, nymph and adult) takes only a single blood meal, except adult males which do
61 not need to feed, but may take a limited amount of blood. After each blood meal, *I. ricinus* drops off to the ground
62 to moult into the next stage or, in the case of adult females, to lay eggs and die. Feeding on a host can last three
63 to six days for larvae, four to seven days for nymphs and seven to ten days for adult females. Other aspects of
64 the life cycle are more geographically variable. Indeed, the *I. ricinus* life cycle can take anywhere from two to four
65 years to complete, depending on environmental conditions and the length of diapause periods (Gray et al. 2021).
66 The questing activity of this tick is regulated by photoperiod and is constrained to temperatures between 5 and
67 30°C and to a minimum relative humidity of 80% (Gray et al. 2021). Nevertheless, despite these generalities,
68 local adaptation of *I. ricinus* populations is known to occur (Gray et al. 2021; Tomkins et al. 2014). The life cycle
69 of *I. ricinus* is triphasic, that is, each stage feeds on a different individual host. It is a generalist (or telotrope) tick
70 in terms of its host range. The composition and abundance of the local vertebrate host population directly
71 influences tick infestation dynamics, relative abundance and dispersal capacities. In turn, this local vertebrate
72 community will affect the transmission dynamics of tick-borne pathogens and their relative prevalence in
73 questing ticks (Hofmeester et al. 2016). Host choice varies according to tick life stage and can be at least partly
74 explained by the height at which *I. ricinus* ticks quest on the vegetation, which itself depends on their relative
75 resistance to desiccation (lowest in larvae and highest in adults), the type of vegetation, and the microclimatic
76 conditions (Mejlon & Jaensen 1997; Randolph & Storey 1999). For example, due to the presence of larval ticks
77 within the leaf litter (where egg laying takes place), small mammals (wood mice, voles and shrews) are often

78 considered as the primary hosts of larvae, followed by passerine birds living in closed habitats (e.g., forest or
79 hedgerows) and feeding on the ground (e.g., blackbirds, thrushes, tits, robin) (Hofmeester et al. 2016). Nymphs
80 are frequently found on birds, lizards, and medium to large mammals, while adult females, which often quest
81 higher on the vegetation, are generally observed only on medium to large mammals (Hofmeester et al. 2016;
82 Mendoza-Roldana & Colella 2019). Indeed, the distribution and abundance of wild ungulates are considered key
83 factors determining the probability of tick exposure (Takumi et al. 2019). Birds can contribute to the
84 dissemination of ticks in the landscape at short, medium and large scales (Vollmer et al. 2011; Marsot et al.
85 2012; Hofmeester et al. 2016). The high variation in the population density of small mammals, itself influenced
86 by tree seed production (masting), is also thought to be an important driver of tick population dynamics at local
87 scales (Perez et al. 2016; Bregnard, Rais & Voordouw 2020). Because of their differential susceptibility to
88 environmental conditions and to variation in ontological processes, the different tick life stages also differ in their
89 seasonal activity periods, with larvae generally appearing later in the season than nymphs and adults (Wongnak
90 et al. 2022). Identifying the main hosts and the timing of tick activity according to the life stage are essential
91 elements for understanding the transmission dynamics of tick-borne pathogens and thus for implementing local
92 prevention measures (Randoph et al. 1999).

93 France covers 552,000 km² in Europe, extending through about 9° of latitude and including a large panel of
94 climatic zones (semi-continental, Mediterranean, oceanic and mountainous zones) and a rich diversity of
95 habitats therein. Climates and environments suitable for the development of *I. ricinus* cover a large part of the
96 territory, thus explaining the broad distribution and major importance of this tick species for both human and
97 veterinary health (Wongnak et al. 2022). Consequently, several studies have been conducted on *I. ricinus* and its
98 associated pathogens in France, but in a piecemeal way, focusing for example on a particular tick-borne disease
99 (e.g. Lyme borreliosis, babesiosis), a particular host group (e.g. cattle, small mammals), or a particular
100 geographic area. The present work represents the first attempt to synthesize available data on *I. ricinus* and the
101 pathogens it transmits in France. On the basis of a systematic literature search, we synthesize knowledge on:

102 1) Host infestation by *I. ricinus*, to detect potential differences in host use within France and among areas in
103 Europe.

104 2) The spatio-temporal distribution of *I. ricinus* in France, to identify possible geographic trends in tick
105 abundance, variation in activity patterns and the influence of environmental factors.

106 3) Tick-borne pathogens detected in *I. ricinus*, to better assess their spatial distribution and variation in exposure
107 risk.

108 Finally, by highlighting knowledge gaps in the ecology of *I. ricinus* and acarological risk in France, we aim to
109 orient future research and preventive measures in this country, and to provide a comparable basis for studies in
110 other regions of *I. ricinus*' distribution.

111

112 **2 Materials and methods**

113 **2.1 Research approach**

114 To retrieve a comprehensive set of available literature on the ecology of *I. ricinus* in France and the pathogens it
115 transmits, we chose a “**Population, Context, Comparators and Outcome**” (PCCO) approach (Livoreil et al.
116 2017). This approach aims (1) to determine the words to use in the literature search and (2) to structure the
117 criteria for including or excluding a reference. Studied populations, contexts, comparators and outcome variables
118 are presented in **Table 1**.

119

120 **Table 1:** Components elements of the literature search.

Component	Elements
Population	Any <i>I. ricinus</i> populations at larval, nymphal or adult stage
Context	European France, i.e. excluding overseas French territories
Comparators	No comparator were excluded. Comparators include, for instance: temporal comparisons, i.e. intra-annual, weather-related and daily; spatial comparisons according to climate (biome), land cover and land use (landscape context and management, habitats, vegetation types, anthropic activities, management); host density and diversity (wildlife management, ex-closure or enclosure, population fluctuation); potential treatments (e.g. acaricide treatments, vaccinations)
Outcome variables	Presence/absence; abundance; density; hosts parasitic burden (presence, prevalence or mean infestation); distribution and dispersal (displacements at different scales, gene flows); behaviour (e.g. questing activity, host preference); search for tick-borne pathogens (presence and/or prevalence)

121

122 The target “**populations**” were *I. ricinus* at all life stages: larvae, nymph and adult. The “**context**” corresponded
123 to European France as the target area (French territories outside the European continent were excluded
124 because they are outside the distributional range of *I. ricinus*) and included the environmental factors of interest
125 identified from both short-term punctual studies and long-term monitoring and from micro-habitat to bio-regional
126 scales. The “**comparator**” corresponds to the kinds of comparisons that could be made with the references. All
127 types of comparators were eligible for the review *a priori*. Expected comparators were spatio-temporal
128 comparisons, including inter-annual (i.e., dynamics), intra-annual (i.e., seasonal variation in questing tick
129 density), and daily comparisons (i.e., abundance according to the hour of the day). Spatial comparisons occurred

130 at multiple scales: micro-habitats, habitats, landscapes and the biogeographic scale. It also included
131 comparisons between vegetation management types, levels of anthropic pressure and/or types of anthropic
132 activities, vertebrate host densities and physical, chemical or biological treatments of the environment or the
133 host. The “**outcome**” variables of interest were those providing information on the ecology of *I. ricinus*: relative
134 abundance in space and time, survival, activity, host use and infestation intensity by life stage, distribution and
135 dispersal. The assessment of tick-borne pathogens in ticks was also considered as an outcome variable.

136

137 **2.2 Search strategy**

138 **2.2.1 Keywords and search lines**

139 The literature search was conducted on titles, abstracts and keywords in English, but references in both English
140 and French were considered. The search line included the name of the species of interest, “*Ixodes ricinus*” and
141 all the outcome variables identified in **Table 1**. The keyword “France” was not included in the search line
142 because the sampling country is not always mentioned in the title or abstract. The keywords “pathogen” and
143 “infectious agents” were not included to avoid references focused only on cellular or molecular aspects of tick-
144 borne pathogens in *I. ricinus*, assuming that the detection of pathogens would have been expressed as presence
145 or prevalence. The final search line was:

146 “***Ixodes ricinus***” AND (**abundance OR activity OR [behaviour OR behavior] OR burden OR density OR**
147 **dispersal OR distribution OR dynamics OR infestation OR presence OR prevalence OR questing**).

148 This search line was adapted to correspond to the different database constraints (see exact search lines in **SI 1**).

149

150 **2.2.2 Databases**

151 The search was conducted between November 14th and December 16th 2019 in the following databases: CAB
152 Direct, JSTOR, Pascal & Francis, PubMed, ScienceDirect, Scopus, WorldCat (see **SI 1** for further details). To
153 access French publications and grey literature, a complementary search was conducted over the same period
154 using “*Ixodes ricinus*” as the unique keyword in the following databases: Agricola, Open Access Thesis and
155 Dissertations, Thèses vétérinaires – i.e. Doctor in Veterinary Medicine (DVM) dissertation theses – (French
156 only), and theses.fr – i.e. PhD theses – (French only). The efficiency of the search strategy was tested using a
157 previously established test-list of 110 references known to be relevant for at least one of the established criterion
158 references (see **SI 2**). To reach a more exhaustive corpus, additional references identified opportunistically and
159 published until 2020 were also considered and submitted to the same eligibility screening (see below).

160 2.3 Eligibility screening

161 2.3.1 Eligibility criteria

162 We retained peer-reviewed research articles and reviews (not including conference proceedings), book sections,
163 veterinary or university theses published at any time prior to December 16th, 2019. Only references in French or
164 English were considered. Screening was conducted by one of the authors (GP), first on titles, then on abstracts,
165 and finally on the full text when available. Finally, studies were included in this systematic review when they met
166 all of the following criteria (see detailed criteria in table **SI 3**):

167 - at the title and abstract stage:

168 **Population:** The reference title must mention *I. ricinus* or ticks or any word suggesting that *I. ricinus* was
169 studied in the paper (e.g., ectoparasites, tick, vector-borne disease). In the latter case, references were
170 retained for subsequent examination (at full text stage).

171 **Context:** Studies must be performed at least in part in France. If the country of study was not mentioned, the
172 reference was retained for subsequent examination (at full text stage).

173 **Comparator:** no type of comparator was excluded.

174 **Outcome:** Studies must be focused directly on the ecology of *I. ricinus*. For example, those that focused on
175 cellular or molecular aspects of *I. ricinus* biology or on tick-borne pathogens alone, were excluded. If there
176 was a doubt, the reference was retained for subsequent examination of the full text.

177 - at full text stage:

178 **Population:** only articles concerning *I. ricinus* were retained, i.e., with at least one mention of the species.

179 **Context:** all references including at least one sample from France, Corsica island or other French islands of
180 the Mediterranean Sea, Bay of Biscay, Celtic Sea, English Channel, and North Sea were retained.

181 **Comparator:** no type of comparator was excluded.

182 **Outcomes:** the same criteria used for the title and abstract stage were applied.

183

184 2.4 Systematic map and narrative synthesis

185 2.4.1 Database for the systematic map

186 A dataset was created, composed of 17 bibliographic fields and 41 descriptive fields. The 41 descriptive fields
187 were filled mainly on the basis of “Materials and methods” and “Results” sections, annexes and supplementary
188 materials of the retained references. These fields described the study type (2 fields), the sampling strategy in

189 time (4 fields) and space (10 fields), the sampling methods (17 fields), the pathogens studied (4 fields) and the
190 explanatory variables (2 fields). A field was added to justify the potential exclusion of the reference, and another
191 field for comments. The dataset, with a detailed fields description, is available in **SI 4**.

192

193 **2.4.2 Narrative synthesis**

194 The narrative synthesis presented the type of collected data, the spatial and temporal scales studied, as well as
195 the abiotic and biotic variables associated with the presence (/absence), abundance and activity of *I. ricinus*. The
196 vertebrate hosts studied and their mean infestation rates by different *I. ricinus* life stages were retrieved from the
197 literature. These data were discussed with respect to existing knowledge on the host species use in Europe.
198 Tick-borne pathogen prevalence per tick life stage was summarised, along with associated detection methods,
199 and distribution maps were established. The collected data on pathogen detection were then discussed taking
200 into account the vector competence of *I. ricinus* and the potential reservoir role of the different vertebrate hosts.

201

202 **3 Results and discussion**

203 **3.1 Reference search results and bibliographic description**

204 **3.1.1 Reference search and screening**

205 The systematic search retrieved 19,654 references, as presented in the PRISMA flow chart (**Figure 1**). This
206 included 3,091 references from CAB Direct, 858 from JSTOR, 662 from Pascal & Francis, 2,102 from PubMed,
207 2,731 from ScienceDirect, 2,473 from Scopus, and 6,174 from WorldCat databases. The complementary search
208 for grey literature in other databases allowed us to identify 1,316 references from Agricola, 150 references from
209 Open Access Thesis and Dissertations, 40 French DVM dissertation theses, and 57 French PhD theses. Only
210 five of the 110 established references from the test-list were not found during our systematic literature search
211 (i.e., 95.4% of references were found). Additionally, 15 references found opportunistically, including five between
212 2019 and 2020, and fulfilled the inclusion criteria.

213 After having discarded 11,298 duplicates (57.4%), 8,370 references underwent title and abstract screening and
214 198 underwent full-text screening for eligibility (**Figure 1**). The most common reasons for exclusion at the title
215 and abstract stage were that sampling was not conducted in France or studies focused on cellular or molecular
216 aspects of *I. ricinus* biology. The most common reasons for exclusion at the full text stage were that studies
217 focused on tick-borne pathogen without reference to the vector (laboratory studies or interactions with the

218 vertebrate host only) (7 cases), or were laboratory-based studies of *I. ricinus* vector competence. In the end, 187
219 references fulfilled the inclusion criteria (SI 5).

220

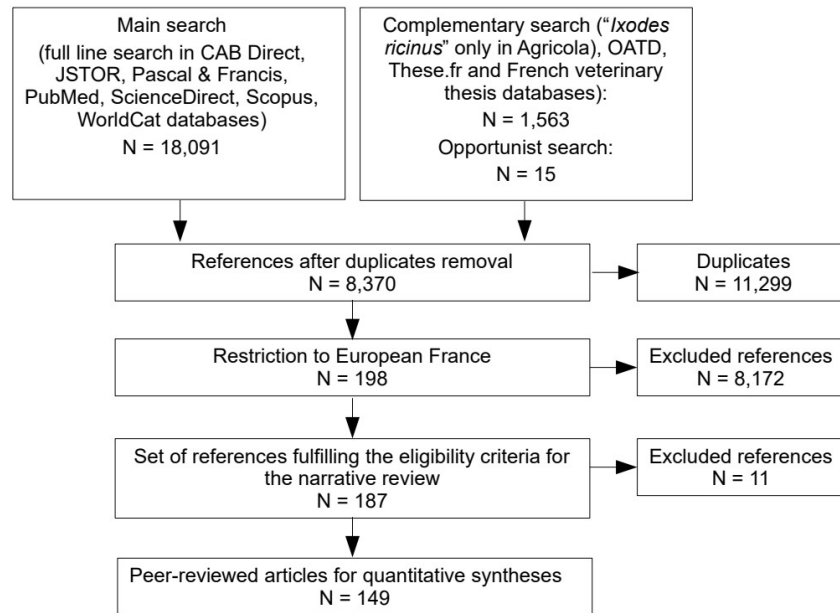


Figure 1

221

222 **Figure 1:** PRISMA-style scheme reporting the literature search and selection strategy arriving to the final 187 references
223 including the 149 peer-reviewed articles used for data compilation.

224

225 3.1.2 Description of eligible references

226 Most of the 187 references were peer-reviewed journal articles and included primary research articles (n = 137,
227 73.3%) and reviews (n = 12, 6.4%), whereas other documents were DVM and Doctor of Pharmacy (PharmD)
228 dissertations (n = 22, 11.8%), PhD theses (n = 15, 8.0%), or book sections (n = 1, 0.5%). Two-thirds of the
229 journal articles were in English (n = 97, 65.1%), while others were in French (n = 52, 34.9%). The oldest
230 reference recorded was published in 1965. References were scarce until the 1990's, slowed-down again in the
231 2000's and then increased again from 2010 onwards (SI 6). The 12 selected reviews provided only a broad
232 overview of ticks and tick-borne diseases or, conversely, a synthesis on some precise aspect of *I. ricinus* ecology
233 and tick-borne diseases in France; none contained a systematic map providing a summary of existing data for
234 the species.

235 Of the peer-reviewed articles, most were based on field data followed by laboratory analyses (e.g., searching for
236 pathogens) (n = 130, 87.2%), but some used field-collected ticks to conduct further laboratory experiments (e.g.,
237 assessing the effect of a variable on tick activity) (n = 3, 2.2%) or laboratory methodological evaluation (n = 4,
238 8.1%). Field studies were mainly exploratory (i.e., considering at least one explanatory variable; n = 68, 45.6%)
239 and case/occurrence reports (i.e., only descriptive; n = 60, 40.3%), but two of them (1.5%) were methodological
240 evaluations of sampling techniques. Among studies followed by experiments, one (0.7%) was conducted to
241 assess the reservoir competence of Siberian chipmunks, *Tamias sibiricus barberi*, for *Borrelia* spp., and two
242 (1.3%) combined field data and laboratory experiments to study tick adaptation to climate. Among laboratory
243 methodological evaluations, three (2.2%) were associated with the development of laboratory methods for
244 pathogen detection, and one (0.7%) was involved the development of a method to study tick population genetics
245 based on field-sampled ticks.

246

247 **3.2 Descriptive synthesis of the ecology of *Ixodes ricinus* in France**

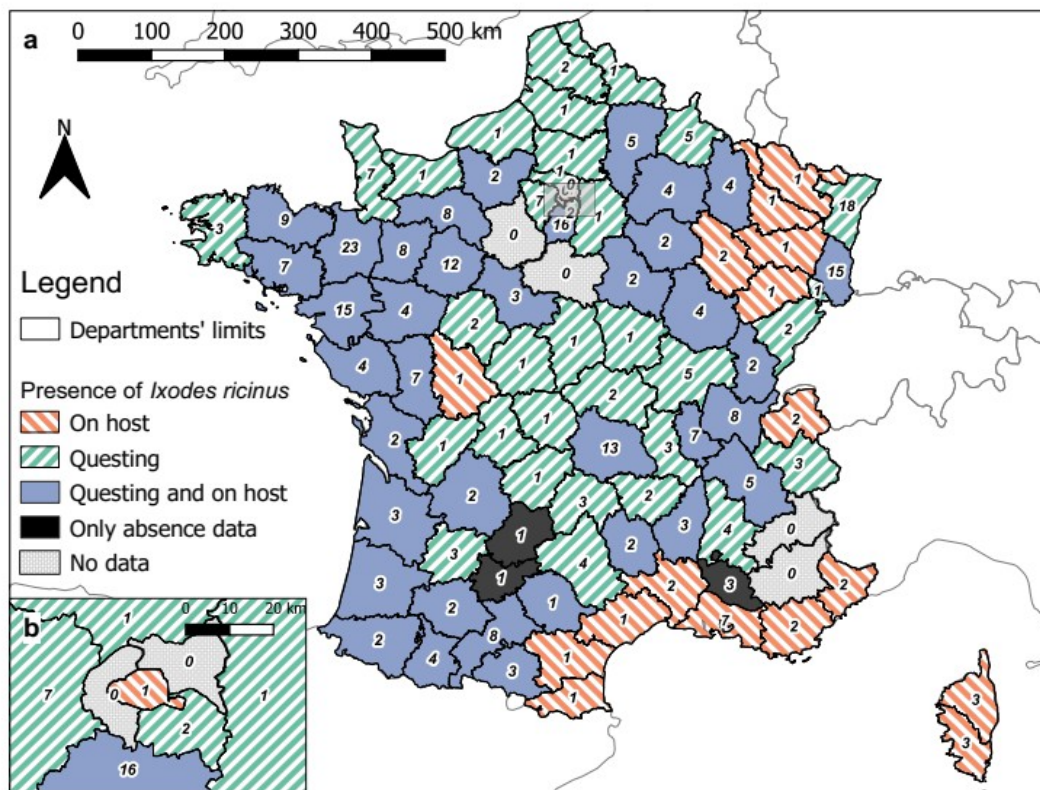
248 **3.2.1 Distribution of *Ixodes ricinus***

249 Over the past fifty years, several studies were conducted to assess the distribution of *I. ricinus* in different
250 regions of France. The presence of *I. ricinus* was reported when ticks were questing on vegetation using the
251 dragging or flagging method (n = 98), attached on a host (n = 59), or both (n = 25). The sampling locations at the
252 department level could be identified in 127 articles. Thus, we used this spatial scale (NUTS-3) to depict the
253 known distribution of the tick species. A distribution map by department was produced from the retrieved data
254 (**Figure 2** and **SI 7**). Sampling effort varied greatly across the territory, with most studies concentrated on the
255 departments of Ille-et-Vilaine (n = 23, Brittany, western), Bas-Rhin (n = 18, Alsace, north-eastern), Essonne (n
256 = 16, Paris region), Loire-Atlantique (n = 15, Pays-de-la-Loire, western), Haut-Rhin (n = 15, Alsace, north-
257 eastern), Puy-de-Dôme (n = 13, Auvergne, central), and Sarthe (n = 12, Pays-de-la-Loire, western). Studies
258 covered 90 out of 96 European French departments. Among these 90 departments, the presence of *I. ricinus*
259 was confirmed in 87 (97.7%).

260 An inventory in the Rhône Valley (south-eastern France) of a 330×80 km area, from Mediterranean sea and
261 northward, recorded the presence of *I. ricinus* in the northern part of the study area, but not the southernmost
262 part (Gilot et al. 1989). In south-western France, in a study that aimed at detecting the presence of *I. ricinus* on
263 100 sites over 15 different vegetation types covering 23 departments, the species was never detected in sites

264 with Mediterranean vegetation (Doche et al. 1993; Gilot et al. 1995). However, in Corsica, Grech-Angelini et al.
265 (2016) reported the species feeding on cattle in areas above 600 m above sea level (a.s.l.) and recently
266 Sevestre et al. (2021) reported the species on hosts and questing in south-eastern France (Alpes-Maritimes)
267 between 450 m and up to 1300 m a.s.l.. Thus, *I. ricinus* ticks seem to be present in some Mediterranean
268 departments, but only under specific environmental conditions and above a certain altitude (Stachurski & Vial
269 2018; Sevestre et al. 2021).

270



271

272 **Figure 2:** Distribution map of *Ixodes ricinus* in European France by departments according to the final 187 references, and
273 whether ticks were questing or attached on host. Refer to **SI 7** for the name of the departments.

274

275 Climate conditions above a certain altitude also limit *I. ricinus*. For instance, Gilot et al. (1989) in the Rhône
276 Valley recorded the species from 200 to 1,150 m a.s.l., but the species was more recently collected at the top of
277 the Pic de Bazès, in the eastern part of the French Pyrenees, at 1,800 m a.s.l. (Akl et al. 2019). These data
278 support other observations in Europe that have shown that its presence is increasingly detected at higher

279 altitudes, beyond the previously established 1,500 m (Gern, Morán Cadenas & Burri 2008; Danielova et al. 2006;
280 Gilbert 2010; Martello et al. 2014; Garcia-Vozmediano et al. 2020).

281 The species was also considered to be scarce on the Atlantic coast because of coastal environmental
282 conditions, like wind and spray which can be highly desiccative (Degeilh et al. 1994). This tick is nonetheless
283 present on Belle-Île-en-Mer island (Bonnet et al. 2007), indicating that the species can be present on islands, but
284 at low abundance. Indeed, ten years after the first study, Michelet et al. (2016) did not collect any *I. ricinus* ticks
285 on this same island.

286 At the landscape level, the presence of the species is associated with wooded areas, either deciduous or
287 deciduous/coniferous mixed forests, small woods, copses and hedgerows in agricultural matrix, and can be
288 found in adjacent grassland and wet meadows. The species is rare in other open habitats, like crops and
289 grasslands, but can be found in public parks depending on their level of forestation (Gilot, Pautou & Moncada
290 1975; Doche et al. 1993; Degeilh et al. 1994; Gilot et al. 1994; Doby & Degeilh 1996; Pichot et al. 1997;
291 Mémeteau et al. 1998; Boyard et al. 2007; Boyard et al. 2011; Agoulon et al. 2012; Perez et al. 2016; Vourc'h et
292 al. 2016; Ehrmann et al. 2017; Goldstein et al. 2018; Mathews-Martin et al. 2020). Landscapes with a moderately
293 fragmented forest, which provides forest-grassland or forest-agriculture ecotones and harbouring high host
294 densities can favour high nymph abundance (Perez et al. 2016; Wongnak et al. 2022).

295

296 **3.2.2 Temporal variation in the density of questing *Ixodes ricinus***

297 Of the 98 articles that sampled questing ticks, 42 analysed temporal variation in tick density, either per sampling
298 area (e.g., nymphs/10m²; n = 31) or per sampling time (e.g., nymphs per hour; n = 11). Both the number of
299 collections and sampling intervals varied strongly among these studies (from a single sample to monthly
300 sampling over several years and from one sample per year to several samples on the same day). Studies have
301 mostly focused on nymphs, with few reports on annual or seasonal activity patterns of larvae. As *I. ricinus* is
302 susceptible to desiccation, weather conditions, and particularly temperature and humidity, were most frequently
303 examined. Here, we report variables that have been linked to variation in *I. ricinus* activity, without assessing
304 potential bias.

305 Temperature is an important factor affecting tick activity. In France, *I. ricinus* activity seems optimal at about 16°C
306 with a very sharp drop below 5°C (Aubert 1975; Tomkins et al. 2014; Cat et al. 2017). Nonetheless, it should be
307 noticed that despite negative temperatures the days before collection (as low as -7°C), attached feeding-ticks
308 are reported on large mammals, possibly activated by the animal's warmth while resting (Doby et al. 1994).

309 Conversely, temperatures above 30°C inhibit tick activity, even if residual activity can persist (Cat et al 2017).
310 More generally, it is the cumulative temperature over several days that affects the activity of *I. ricinus* (Perret et
311 al. 2000; Tagliapietra et al. 2011). For instance, in north-eastern France, adult tick feeding activity – estimated by
312 individuals found feeding on foxes – was triggered by a 10-day mean maximum temperature above 9°C prior to
313 the fox hunt, while a mean minimum 10-day temperature below 1°C inhibited it (Aubert 1975). It is nonetheless
314 important to note that threshold temperatures for tick activity could vary among climates if tick populations
315 undergo local adaptation, with ticks remaining active at lower temperatures in colder climatic regions for example
316 (Tomkins et al. 2014; Gilbert et al. 2014).

317 Combined with temperature, humidity is also an important limiting factor for the survival and activity of *I. ricinus*
318 ticks. It is generally considered that ticks need a relative humidity greater than 70-80% to maintain water balance
319 (Gray et al. 2016). Therefore, ticks regularly interrupt host-seeking activity and move down to moist litter to
320 rehydrate. Saturation deficit, which integrates both relative humidity and temperature, is considered as a better
321 predictor of tick activity than temperature or humidity alone (Perret et al. 2000; Hauser et al. 2018). In France, it
322 was reported that the activity of *I. ricinus* nymphs could be partially predicted by the mean 7-day minimal relative
323 humidity, and marginally by precipitation in the four weeks prior to sampling, two determinants of the water
324 available in the environment (Paul et al 2016; Cat et al. 2017).

325 Photoperiod can also drive questing activity of *I. ricinus* as it influences the beginning of developmental diapause
326 and the end of behavioural diapause (Gray et al. 2016). Briefly, decreasing daylight induces a developmental
327 diapause in eggs and fed larvae and nymphs, delaying development for at least three months, and results in a
328 behavioural diapause of tick activity (Perret et al. 2003). Conversely, increasing daylight triggers tick activity for
329 nymphs and adults. Darkness is favourable for the horizontal displacement of ticks, likely because it is generally
330 associated with a reduction in desiccation risk (Perret et al. 2003).

331 As daylight, temperature and humidity change daily, tick activity is subject to daily variation. Recent results from
332 eastern France (near the city of Lyon, Rhône) suggest that *I. ricinus* nymphal activity in spring decreases during
333 the day (between 7 am and 4 pm) with increasing temperatures and decreasing humidity (Kraemer 2018).
334 Another study, carried out in south-western France (Haute-Garonne), suggested that ticks were more active
335 during the afternoon (3-6 pm) in winter, at the end of the day in spring and summer, and remained active at night
336 in summer, as long as temperature and humidity are favourable (Coiffait 2019). These results are concordant
337 with other studies in Europe showing increasing activity after sunrise in cold months, decreasing activity and shift
338 in activity toward the night in hot months (Mejlon 1997; Zöldi et al. 2013; Edwards & Campbell 2021). Nocturnal

339 activity in summer could explain an increase in tick infestation of nocturnal and crepuscular host species like red
340 foxes (Aubert 1975).

341 It was hypothesized that daily tick activity is adapted to host activity to increase encounter rate. For instance,
342 Matuschka et al. (1990) observed in laboratory conditions that larvae feeding on different host species detached
343 at different periods of the day, but whether this is an effect of host activity (e.g., grooming, exploratory
344 movements) or a behavioural adaptation remains unknown. Recently, in south-western France, Coiffait (2019)
345 compared the daily activity of adult ticks with the daily activity of roe deer, *Capreolus capreolus*, which have a
346 crepuscular activity, but found no relationship. However, these preliminary results need to be confirmed insofar
347 as roe deer behaviour itself can be modified in anthropic landscapes (Bonnot et al. 2013). More data are thus
348 needed on the influence of local host community on tick activity of all stages.

349 Given these dependencies, tick activity may vary strongly over a year and under different climates, resulting in
350 seasonal and geographical variation in exposure risk for humans and their domestic animals. In France, the
351 general phenology of *I. ricinus* seems to be the same as in other parts of Europe under the same climates
352 (Kurtenbach et al. 2006). In temperate oceanic and temperate semi-continental climates, the activity peak of
353 larvae is generally reached in late spring or summer, depending on meteorological conditions (L'Hostis et al.
354 1995; Agoulon et al. 2019; Bournez et al. 2020). However, data on larval activity are scarce and differences in
355 phenology should be confirmed. Moreover, vegetation height can bias larval sampling, which typically quest low
356 in the vegetation (Dobson et al. 2011). Larvae are scarce or absent in winter, suggesting that even if a female
357 tick feeds and lays in late autumn or early winter, hatching occurs only in spring (L'Hostis et al. 1995). Under
358 climates with mild temperatures throughout the year, as in the temperate oceanic climate of western France,
359 nymphs can be found throughout the year since the required minimum favourable abiotic conditions are met
360 (Agoulon et al. 2019). Under these climates, the peak in nymphal activity occurs between March and June (Cat
361 et al. 2017; Degeilh 1996; Agoulon et al. 2019). This peak can be delayed in years with mild springs and
362 shortened by high local host densities that rapidly remove ticks from the questing population (Randolph and
363 Steele 1985; Vassallo, Paul & Pérez-Eid 2000). Under semi-continental climates, the peak of nymphal activity is
364 observed in May-June (Pérez-Eid 1989; Ferquel et al. 2006; Beytout et al. 2007; Goldstein et al. 2018; Bournez
365 et al. 2020a) with no (or very few) questing nymphs found during the cold season. A weaker peak of activity was
366 sometimes observed in September-October (L'Hostis et al. 1995; Degeilh et al. 1996; Cat et al. 2017; Lejal et al.
367 2019b); this second peak could result from the emergence of larvae fed in spring rather than to the revived
368 activity of nymphs which survived the summer (Randolph and Steele 1985; Bregnard et al. 2021). Under

369 mountainous climates, a unique peak of activity is observed in summer (Jouda, Perret & Gern 2004). As adults
370 are less susceptible to desiccation than immature stages (Perret, Rais & Gern 2004), their activity tends to be
371 more widespread through the year (Pérez-Eid 1989), but still follows the same general pattern as nymphs
372 (Aubert 1975; Degeilh et al. 1996; L'Hostis et al. 1996a; L'Hostis et al. 1996b; Marchant et al. 2017; Goldstein et
373 al. 2018; Agoulon et al. 2019). Under Mediterranean climates, like in Corsica, the peak in adult activity is in
374 autumn, while data on larval and nymphal activity are lacking (Grech-Angelini et al. 2016).

375 To study the trends in population dynamics of *I. ricinus*, long-term data are needed to dampen year-to-year
376 variation. Paul et al. (2016) sampled questing ticks every spring between 2008 and 2014 in a suburban forest in
377 the Paris region (Essonne). This study reported that main climatic variables explaining inter-annual variation in
378 the density of questing ticks were the number of days below zero degrees within a year and minimal
379 temperatures 8-9 months prior to tick collection. Thus, low winter temperatures, but also large temperature
380 variation in winter and extreme climatic events could have a negative effect on tick survival, explaining part of the
381 annual variation in tick density (Herrmann & Gern 2013; Paul et al. 2016; Hauser et al. 2018). However, in Paul
382 et al. (2016), inter-annual fluctuations in questing nymph density were considered to be more closely linked to
383 fluctuations in vertebrate host densities and vegetation cover than to meteorological data per se. Similar
384 inferences were made in longitudinal studies performed in Switzerland and Germany (Brugger et al. 2018;
385 Hauser et al. 2018; Bregnard, Rais & Voordouw 2020). Perez et al. (2016) also reported that nymphal density
386 was associated with both the presence of larvae and the abundance of small mammals the previous year. Larval
387 density was itself associated with the proportion of woodlands in the surrounding landscape, a privileged habitat
388 for roe deer, which are the main hosts of adult females (Perez et al. 2016; Morellet et al. 2011).

389 Despite some studies documenting a northward and altitudinal expansion of *I. ricinus* in Europe, probably linked
390 to climate changes, few sampling campaigns have been conducted over a sufficiently long time period to test an
391 effect of climate change on tick abundance at more local scales (Lindgren et al.; 2000; Léger et al. 2013;
392 Medlock et al. 2013). To our knowledge, the longest *I. ricinus* yearly population survey, conducted in the eastern
393 part of the species range (Tula region, western Russia) between 1977 and 2011, showed a general increase in
394 adult abundance since 1990 in relation to an increase in degree days (cumulated daily temperature) during the
395 August-October period. This increase was also associated with changes in forest coverage and fragmentation
396 observed in the region following socio-economic changes (Korotkov, Kozlova & Kozlovskaya 2015). Thus, while
397 weather conditions have an influence on annual tick population densities, hosts and landscape changes seem to
398 have an influence as well. These factors are nonetheless difficult to disentangle since they generally interact.

399

3.2.3 Host use

400 Out of 59 articles reporting tick sampled on hosts, only 33 (55.9%) presented sufficient details to be informative
401 on host-associated infestation rates. The potential vertebrate host species of *I. ricinus* studied in France and the
402 degree of parasitism by each life stage is presented in (SI 8). Overall, 55 species were examined for the
403 presence of *I. ricinus* ticks. These species included 29 mammalian species (4 Carnivora, 8 Cetartiodactyla, 4
404 Eulipotyphla, 1 Lagomorpha, 1 Perissodactyla and 11 Rodentia) reported in 34 articles, and 26 avian species (24
405 Passiformes and 2 Piciformes) reported in 4 articles. No data on Squamata (i.e., lizards and snakes) were found.
406 More detailed data on parasitism (i.e., infesting life stages and/or prevalence/intensity of infestation) were
407 available in 26 articles for mammalian hosts, but in only two studies for avian hosts. In the first avian study, 21
408 different avian species were included (Marsot et al. 2012), while in the second one, only the Eurasian blackbird,
409 *Turdus merula*, was considered (Grégoire et al. 2002).

410 Data from different studies preclude direct comparisons of host infestation levels because biogeographic zones
411 and sampling season usually differ from one study to another. For instance, wild ungulates are typically studied
412 in winter, during the hunting season, when ticks are less active (Doby et al. 1994), whereas birds are captured in
413 spring, when ticks are highly active (Marsot et al. 2012), and small mammals are trapped from spring to autumn
414 (L'Hostis et al. 1996b; Perez et al. 2016). In addition, it is not possible to compare levels of host infestation when
415 comparing areas where *I. ricinus* is very frequent, like in the northern part of France (Pérez-Eid 1990; Doby et al.
416 1994; L'Hostis et al. 1996b) to areas where this species is very rare, like in Corsica (Grech-Angelini et al. 2016).
417 Finally, the modalities (e.g., time of inspection, body part inspected) of tick collection on hosts also varies from
418 one study to another. For instance, wild boars, *Sus scrofa*, were inspected only five minutes in the field (Doby et
419 al. 1994), while red foxes *Vulpes vulpes* were meticulously inspected in laboratory (Aubert et al. 1975). These
420 limits highlight the need to standardize studies, controlling for spatial and temporal factors, and employing
421 comparable on-host sampling strategies. For instance, two countrywide standardised studies based on tick
422 collections on red squirrels, *Sciurus vulgaris*, confirmed that *I. ricinus* is rare under Mediterranean climates
423 compared to Atlantic, semi-continental and mountainous climates (Romeo et al. 2013; Pisanu et al. 2014).

424 The proportion of each *I. ricinus* life stage present on a given host species at a given time, can nonetheless
425 provide some indication on their role as blood source and can enable us to formulate testable hypotheses for
426 future work. On small rodents (except for Eurasian red squirrels and Siberian chipmunks), larvae were
427 predominant whereas nymphs were rare (Anderson et al. 1986; Doby et al. 1992; L'Hostis et al. 1996b; Richter
428 et al. 2004; Vourc'h et al. 2007; Boyard, Vourc'h & Barnoin 2008; Marsot et al. 2013; Romeo et al. 2013; Pisanu

429 et al. 2014; Le Coeur et al. 2015; Perez et al. 2017; Pérez-eid 1990; Bournez et al. 2020a). Among rodents, adult
430 ticks were observed only on black rats, *Rattus rattus*, from Corsica (Cicculi et al. 2019). We can note that this
431 observation questions the role of black rats in transporting ticks in peri-urban and urban areas.

432 Larvae and nymphs were frequent on passerine birds, with sometimes more nymphs than larvae (Grégoire et al.
433 2002; Marsot et al. 2012). In eastern France, Grégoire et al. (2002) found that blackbirds were significantly more
434 infested in rural habitats (74%) compared to urban habitats (2%). This suggests a scarcity of ticks in urban areas
435 compared to rural woodlands, but also a possible role of these posted hosts in disseminating ticks in urban and peri-
436 urban green spaces. A similar pattern was observed when comparing tick densities in a reference forest plot and
437 peri-urban and urban parks in the City of Lyon (eastern France); ticks were more abundant in the forest plot than
438 in the peri-urban and in urban parks (Mathews-Martin et al. 2020).

439 Females, nymphs and larvae were all observed on wild ungulates, sometimes with more adults than nymphs
440 (e.g., roe deer, red deer, *Cervus elaphus*, and Pyrenean chamois, *Rupicapra pyrenaica*) (Davoust et al. 2012;
441 Doby et al. 1994; Gilot et al. 1994a). Domestic ungulates can also host numerous female ticks with up to 73 per
442 individual on cattle (L'Hostis, Bureaud & Gorenflot 1996). However, there is no strong evidence that domestic
443 ungulates contribute to an increase of *I. ricinus* populations. For instance, Ruiz-Fons et al. (2012) found a
444 positive relationship of horse abundance with questing larvae, but not nymph, abundance, and Sprong et al.
445 (2019) found a weak negative relationship of cattle abundance with questing adult abundance, while Steigedal et
446 al. (2013) found a negative relationship of sheep presence with nymph and adult abundance. However, in neither
447 case the authors quantified ticks on cattle, horse or sheep, although they may had removed a significant part of
448 the questing ticks (Randolph & Steele 1985). Furthermore, Ruiz-Fons et al. (2012) and Sprong et al. (2019)
449 found a positive relationship of cattle abundance with *Anaplasma phagocytophilum* prevalence, a pathogen for
450 which cattle are reservoir hosts, suggesting that they had fed a significant part of the tick population.

451 Few studies were performed and report *I. ricinus* ticks from wild carnivores in France and all were on foxes
452 (Aubert et al. 1975; Doby et al. 1991). Given their low density compared to other host species, their contribution
453 in feeding ticks is likely low (Hofmeester et al. 2016). The presence of wild Carnivores might even have a
454 negative effect on tick populations due to the predation pressure and behavioural modifications they exert on
455 larvae hosts such as small mammals (Hofmeester et al. 2017). More studies are needed to evaluate the
456 importance of wild Carnivores in the population dynamics and maintenance of *I. ricinus* populations.

457 Studies on domestic Carnivores have focused mainly on infested dogs and cats and frequently fail to report
458 sampling effort, precluding an estimate of infestation level (Panas et al. 1976; Pichot et al. 1997; Gilot, Pichot &

459 Doche 1989; Ulmer et al. 1999; Geurden et al. 2018; Grech-Angelini et al. 2016). However, cats and dogs can
460 be highly infested, with up to 26 and 64 *I. ricinus* ticks, respectively (Geurden et al. 2018). Infestation levels of
461 domestic Carnivores are also influenced by environmental conditions. For instance, Martinod, Brossard &
462 Moreau (1985) showed that dog infestation by *I. ricinus* varied greatly between two areas in a 40 km² zone in
463 eastern France (southern Jura mountains) in relation to land use (5.3 and 0.032 *I. ricinus* adult ticks per dogs on
464 249 dogs from areas with pastures and residential neighbourhoods and 190 dogs from mountainous and plain
465 areas). Like domestic ungulates, the contribution of domestic Carnivores to the population dynamics of *I. ricinus*
466 is unclear. Indeed, domestic vertebrates may act as ecological traps for ticks because of their breeding
467 conditions (housing, antiparasitic treatments).

468 Despite limited data, observations on host use in France are in general agreement with what is known for the
469 host range of *I. ricinus* across its range (Hofmeester et al. 2016). However, more data is required to better
470 understand the relative contribution of these different host types and to evaluate the contribution of understudied
471 groups (Eulipotyphla, Lagomorpha, Perissodactyla and Squamata) in France and elsewhere.

472

473 **3.3 Tick-borne pathogens in *Ixodes ricinus* ticks of France**

474 Different tick-borne pathogens, that have been examined in *I. ricinus* ticks in France, are briefly presented below
475 (see McCoy & Boulanger for more details). We summarised existing data from across studies and present these
476 data in detail in the Supplementary Information (**SI 9-17**). Not enough data exist to establish prevalence maps for
477 most pathogens (with the exception of *Borrelia burgdorferi* s.l.), but presence/absence information is illustrated
478 (**Figures 3-10**).

479

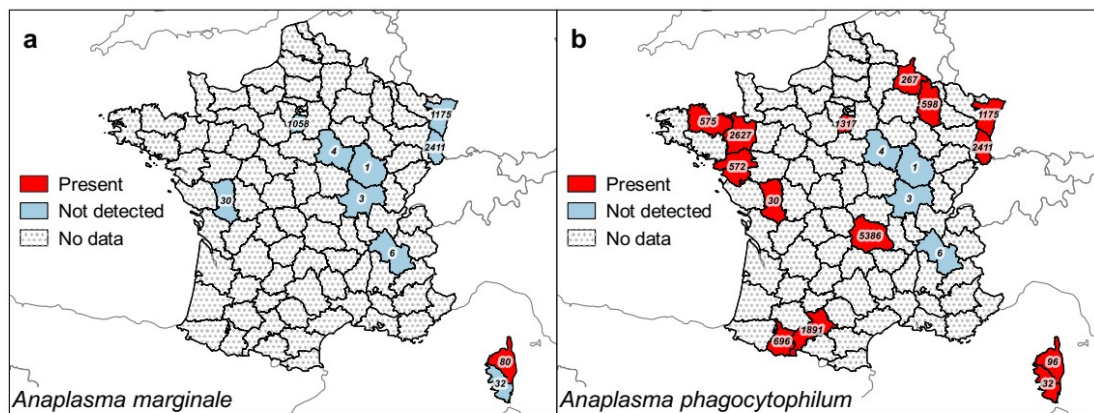
480 **3.3.1 The genus *Anaplasma***

481 Bacteria of the genus *Anaplasma* are obligate Gram-negative alphaproteobacteria. They are intracellular
482 pathogens transmitted by ticks and responsible for anaplasmoses in vertebrates. Among this genus,
483 *A. phagocytophilum* is the most prevalent species in northern Europe and infects monocytes and granulocytes of
484 ruminants, small mammals, horses, canids, birds and humans (Keesing et al. 2012). Several genetic variants
485 circulate in Europe with some host and vector specificities. Jahfari et al. (2014) identified four genetic variants
486 called “ecotypes” associated with different host groups in Europe. According to these authors, ecotype I is
487 associated with ungulates, dogs, hedgehogs and humans; ecotype II is associated mainly with roe deer; ecotype
488 III is associated with rodents; and ecotype IV is associated with birds, results confirmed by other studies (Jahfari

489 et al. 2014; Stigum et al. 2019; Grassi et al. 2021). These ecotypes also differ by their vectors. Ecotypes I and II
490 are mainly transmitted by *I. ricinus*; ecotype III seems mainly transmitted by *I. trianguliceps*; vectors of ecotype
491 IV are still uncertain, but are suspected to be among the hard ticks that specifically exploit birds; and an ecotype
492 IV-like was associated with *I. ventalloi*, a tick species mostly feeding on European rabbits, *Oryctolagus cuniculus*,
493 and present in France (Gilot, Rogers & Lachet 1985; Santos et al. 2018; Jaarsma et al. 2019). Transmission of
494 some genetic variants by ticks of the genus *Dermacentor* is suspected, but has not been demonstrated
495 (Baldrige et al. 2009). Other tick species might be vector of other specific genetic variants. Anaplasmoses can
496 be of significant medical and economic importance when infecting humans and livestock. It may cause severe
497 disease marked by anemia and leukopenia, fever, headache, and myalgia (Rymaszewska & Grenda 2008;
498 Stuen et al. 2013; Dugat et al. 2015). Few human cases are diagnosed in France, and occur mainly in the
499 eastern part of the country (Koebel et al. 2012).

500 DNA of *A. phagocytophilum* bacterium has been detected by PCR methods in questing *I. ricinus* from almost all
501 regions of France and prevalence in ticks shows some geographic disparities (**Figure 3; SI 9** and references
502 associated therein), which may be explained, in part, by wild and domestic ungulate densities (Chastagner et al.
503 2017). Prevalence varied from 0.4% to 5.3% in questing nymphs and from 0.5% to 7% in questing adults.

504



505

506 **Figure 3:** Presence maps of *Anaplasma marginale* and *A. phagocytophilum* in questing and attached nymph and adult
507 *Ixodes ricinus* ticks in European France by department.

508 Detected presence by PCR methods and respective sampling effort per department in number of tested ticks (nymphs and
509 adults) for *A. marginale* (a) and *A. phagocytophilum* (b).

510

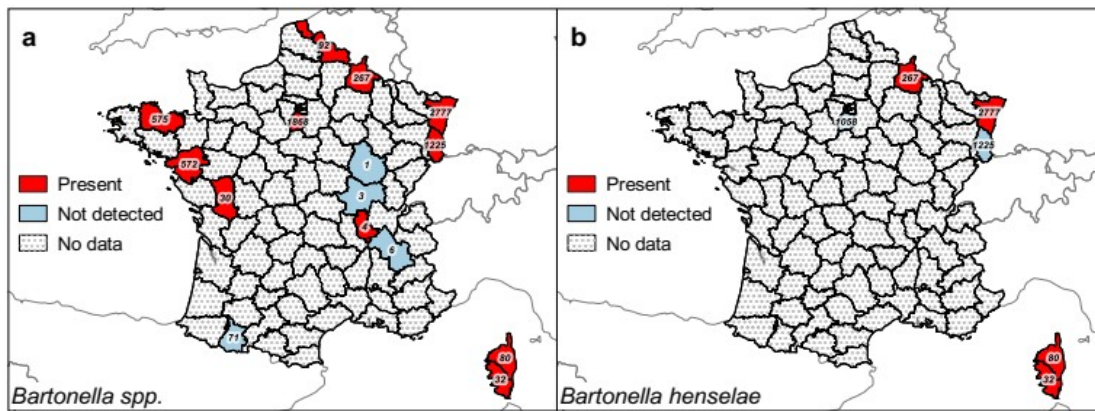
511 Only five studies have attempted to detect DNA of other *Anaplasma* species in questing *I. ricinus* ticks in France
512 (Bonnet et al. 2013; Michelet et al. 2014; Lejal et al. 2019a; Lejal et al. 2019b; Grech-Angelini et al. 2020a).
513 These other *Anaplasma* species infecting animals are *A. centrale*, *A. marginale* and *A. ovis*, infecting
514 erythrocytes of ruminants, *A. (Ehrlichia) bovis*, infecting monocytes and granulocytes of ruminants, and
515 *A. (E.) platys* infecting mainly platelets of dogs (Rymaszewska & Grenda 2008). However, *I. ricinus* is not
516 considered to be the vector of these pathogens. Among these other species, *A. marginale* was detected in only
517 one study in *I. ricinus* ticks feeding on cattle and red deer in Corsica with a prevalence of 1.7% (Grech-Angelini
518 et al. 2020a). The presence of these other *Anaplasma* species in *I. ricinus* ticks in France is thus currently
519 anecdotal (*A. marginale*) (see **SI 9** for further details).

520

521 **3.3.2 The genus *Bartonella***

522 The *Bartonella* genus is composed of facultative intracellular bacteria transmitted by arthropods such as fleas,
523 lice, haematophagous Diptera, and Acari including ticks, and occurs worldwide (Billeter et al. 2008). Known
524 reservoirs are cats, canids and rodents (Chomel, Boulouis & Breitschwerdt 2004). The main pathogenic species
525 for humans are *B. bacilliformis*, *B. henselae* and *B. quintana* (Angelakis & Raoult 2014), but only *B. henselae* is
526 of known concern in France. It is responsible for cat-scratch disease which is usually characterized by mild
527 symptoms (aches, malaise), but can sometimes lead to more severe symptoms like endocarditis or
528 meningoencephalitis. Although *B. henselae* is mainly transmitted among the cat reservoirs via fleas
529 (*Ctenocephalides felis felis*) (Chomel et al. 1996), *I. ricinus* is an experimentally confirmed vector and other tick
530 species and haematophagous Diptera are suspected vectors (Billeter et al. 2008; Cotté et al. 2008; Grech-
531 Angelini et al. 2020a; Wechtaisong 2020). The species *B. birtlessi* that infect rodents is also transmitted by
532 *I. ricinus*, but is likely not pathogenic for humans (Reis et al. 2011b).

533 In France, *Bartonella* spp. have been found from different departments, but with limited sampling effort
534 (**Figure 4a; SI 10**). The bacterium *B. henselae* was the most frequently detected *Bartonella* species in *I. ricinus*,
535 varying from 0% to 38% (**Figure 4b; SI 10**). DNA of this bacterium was found in questing nymphs and adults
536 sampled in north-eastern France (Ardennes and Bas-Rhin) (Dietrich et al. 2010; Michelet et al. 2014; Moutailler
537 et al. 2016b), and in feeding adult ticks in Corsica (Grech-Angelini 2020a). In the Paris region (Essonne), DNA of
538 *B. birtlesii* was detected in questing *I. ricinus* nymphs (Reis et al. 2011b). Other *Bartonella* spp. have been
539 detected in other parts of France, but without an identification to species (Halos et al. 2005; Cotté et al. 2010;
540 Davoust et al. 2012; Bonnet et al. 2013; Paul et al. 2016; Bonnet et al. 2017; Nebbak et al. 2019).



541

542 **Figure 4:** Presence maps of *Bartonella* spp. and *B. henselae* alone in questing and attached nymph and adult *Ixodes ricinus*
543 ticks in European France by department.

544 Detected presence by PCR methods and respective sampling effort per department in number of tested ticks (nymphs and
545 adults) for *Bartonella* spp. (a) and *B. henselae* alone (b).

546

547 3.3.3 *Borrelia burgdorferi* sensu lato (s.l.) complex

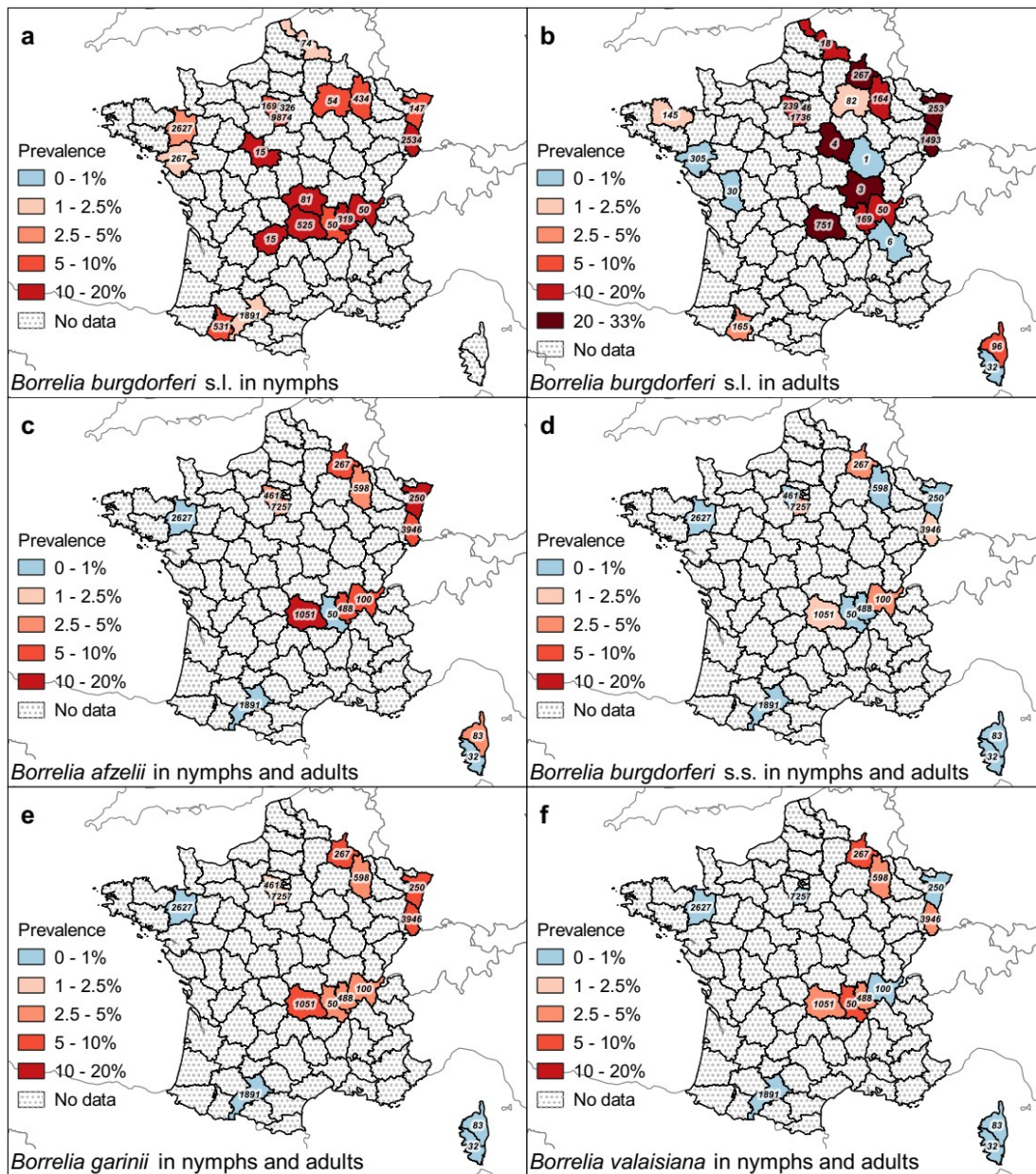
548 Some bacterial species of the *B. burgdorferi* s.l. complex are responsible for Lyme borreliosis, the most important
549 vector-borne disease for humans in the northern hemisphere (Borchers et al. 2015) and that most frequent in
550 France. In 2020, the French national surveillance programme estimated a mean incidence of 90 cases / 100,000
551 inhabitants, varying between 11 and 667 cases/ 100,000 inhabitants depending on the region
552 (<https://www.sentiweb.fr>). In Europe, several genospecies (genetically-discriminated species) of the complex
553 circulate in different reservoir hosts and can be associated with different pathogenicity (Steinbrink et al. 2022).
554 Small mammal-associated genospecies include *B. afzelii*, *B. garinii* subsp. *bavariensis*, *B. bissettii*, and
555 *B. spielmanii*, whereas *B. garinii garinii*, *B. turdi*, and *B. valaisiana* are considered to be bird-associated.
556 *B. burgdorferi* sensu stricto (s.s.) is harboured by both small mammals and birds, whereas *B. lusitaniae* is mostly
557 associated with lizards. There is no known reservoir host for *B. finlandensis* (Wolcott et al. 2021). The species
558 most frequently involved in human cases of Lyme borreliosis in Europe are *B. afzelii* and *B. garinii* (Stanek &
559 Reiter 2011), causing cutaneous and neurological forms of the disease respectively (Strle et al. 2006). Both
560 *B. burgdorferi* s.s. and *B. garinii* subsp. *bavariensis* (formerly *B. garinii* OspA serotype 4, but not differentiated
561 from *B. garinii garinii* in all studies; Hördt et al. 2020) are less frequent in Europe, but are also disease-causing;
562 *B. burgdorferi* s.s. is associated with neurological and arthritic forms of Lyme borreliosis, whereas *B. garinii*
563 subsp. *bavariensis* only manifests neurological forms (Wilske et al. 1996; Margos et al. 2013). Other circulating

564 genospecies like *B. spielmanii*, *B. bissettii*, *B. lusitaniae* and *B. valaisiana* rarely cause human borreliosis
565 (Steinbrink et al. 2022). The genospecies *B. finlandensis* and *B. turdi* are only rarely detected in *I. ricinus* ticks
566 and their pathogenicity for humans is unknown (Steinbrink et al. 2022). The role of *I. ricinus* as a vector has been
567 experimentally demonstrated for *B. afzelii*, *B. garinii* and *B. burgdorferi* s.s. (Eisen 2020).

568 DNA from different *B. burgdorferi* s.l. genospecies, except *B. garinii* subsp. *bavariensis*, *B. bissettii* and
569 *B. finlandensis*, has been detected in questing *I. ricinus* ticks collected in France (**SI 11**). Although studies on
570 *B. burgdorferi* s.l. have focused on a few French departments, the highest prevalence to date is found in the
571 north-eastern, eastern and central parts of France, where prevalence ranges from 2.0 to 26.2% in nymphs
572 (**Figure 5a** and **5b**; **SI 11** and references therein). The prevalence of the different genospecies in questing
573 nymphs can be compared between regions from which a sufficient number of ticks were tested. In the north-
574 eastern quarter of France, *B. afzelii* was the most frequently detected genospecies (35-50% of positive ticks) and
575 the only one in Corsica (**Figure 5c**). The prevalence of *B. burgdorferi* s.s. was generally found to be low across
576 France. However, in one study in northern France, it was the predominant species (32% of positive ticks); the
577 authors suspect that the high prevalence of this genospecies might result from the introduction of the Siberian
578 chipmunk in the sampled forest, which is a competent reservoir with a higher tick burden than local rodent
579 species (**Figure 5d**) (Pisanu et al. 2010; Marsot et al. 2011; Jacquot et al. 2014; Bonnet et al. 2015; Jacquot et
580 al. 2016). This genospecies was also the most predominant in southern France (32%) where the overall
581 *B. burgdorferi* s.l. prevalence was low. In north-western France, *B. garinii* was the genospecies most frequently
582 detected (26%), but at low prevalence compared to those observed in the north-eastern quarter of France, again
583 because of an overall low *B. burgdorferi* s.l. prevalence (**Figure 5e**). The prevalence of *B. valaisiana* varied
584 between 0 and 21% of positive ticks, but did not follow any clear pattern in prevalence (**Figure 5f**).

585 The higher *B. burgdorferi* s.l. prevalence observed in north-eastern, eastern and central regions can be
586 explained by their high proportion of forested landscapes that support higher wild vertebrate densities, in
587 particular wild ungulates (that are good amplifiers of ticks), and wild rodents and birds (reservoirs of the
588 bacteria), compared to northern and western regions with more open landscapes and less forested areas. Given
589 the strong host specificity of genospecies, regional disparities in prevalence in questing nymphs suggests that
590 tick host use differs between regions with different climates, landscapes and host communities. For instance, the
591 proportion of *Borrelia* species harboured by avian species (e.g., *B. garinii*) seems higher in western regions and
592 those harboured by small mammal species (e.g., *B. afzelii*) seem higher in north-eastern regions. Nonetheless,

593 when considering genospecies prevalence, these results are mostly in accordance with the E-W geographical
 594 gradients in *B. burgdorferi* s.l. prevalence observed across Europe (Strnad et al. 2017).
 595



596

597 **Figure 5:** Prevalence maps of *Borrelia burgdorferi* sensu lato and *B. afzelii*, *B. burgdorferi* sensu stricto, *B. garinii*, and
 598 *B. valaisiana* in questing and attached nymph and adult *Ixodes ricinus* ticks in European France by department.

599 Prevalence, corresponding to the minimum detected prevalence by PCR methods, and sampling effort by department, in
 600 number of tested ticks, for *B. burghdorferi* s.l. in nymphs (**a**) and in adults (**b**), and in nymph and adult ticks together for the
 601 genospecies *B. afzelii* (**c**), *B. burgdorferi* s.s. (**d**), *B. garinii* (**e**) and *B. valaisiana* (**f**).

602 The *B. burgdorferi* s.l. prevalence was also found to vary from site to site and from year to year within regions
603 (Boulanger et al. 2018). For instance, in a four-year follow-up on four sites in Alsace region, Boulanger et al.
604 (2018) reported prevalence varying from 0.7% to 13.6% between sites in the same year, and from 7.7% to
605 26.7% between years for the same site. Studies at landscape and local scales suggest that pathogen prevalence
606 is positively associated with wooded habitat ecotones (Halos et al. 2010; Perez et al. 2020), but negatively to
607 habitat diversity (Ehrman et al. 2018). This may be explained by differences in the proportion of each host group
608 used by larvae, which might also vary temporally because of high fluctuations in small mammal population sizes
609 (Perez et al. 2017).

610

611 **3.3.4 *Borrelia miyamotoi* bacterium**

612 The bacterium *B. miyamotoi* is currently the only known species among *Borrelia* relapsing fever (RF) bacteria to
613 be transmitted by a hard tick in Europe; soft ticks and lice are the vectors of the other species of this group
614 (Platonov et al. 2011; Wagemakers et al. 2015). Suspected reservoir hosts are rodents, but these bacteria can
615 also infect some bird species (e.g., wild turkeys, *Meleagris gallopavo*, common blackbirds) and large mammals
616 (roe deer, wild boars) (Wagemakers et al. 2015). In humans, *B. miyamotoi* is responsible for acute febrile illness
617 and meningoenzephalitis (Wagemakers et al. 2015) and the number of human cases reported is continuously
618 increasing in Europe (Henningsson et al. 2019; Tobudic et al. 2020). It has been detected in *Ixodes* ticks,
619 including *I. ricinus*, from different regions of the Northern Hemisphere, and, in contrast with other *Borrelia* spp.,
620 trans-ovarial transmission in ticks is thought to occur (Wagemakers et al. 2015; van Duijvendijk et al. 2016).

621 DNA of *B. miyamotoi* was formally detected by PCR methods for the first time in north-eastern France
622 (Ardennes), both in samples from bank voles (four positive rodents out of 72 tested – 5.5%) and from questing
623 adult female *I. ricinus* ticks (eight positive out of 267 tested – 3.0%) (Cosson et al. 2014; Moutailler et al. 2016b).

624 The presence of this bacterium was subsequently detected by PCR methods in the Paris region, in north-eastern
625 France (Alsace, Champagne-Ardenne), and in Corsica island, with observed prevalence varying between 0.75
626 and 4.2% in questing nymphs and between 0 and 21.7% in adults (**SI 12**) (Vayssier-Taussat et al. 2013; Paul et
627 al. 2016; Boulanger et al. 2018; Lejal et al. 2019a; Lejal et al. 2019b; Nebbak et al. 2019; Boyer et al. 2020).
628 Other RF *Borrelia* sp. have been detected in north-eastern France (Alsace region) that could be *B. miyamotoi*,
629 but the species was not identified (Richter, Schlee & Matuschka 2003).

630

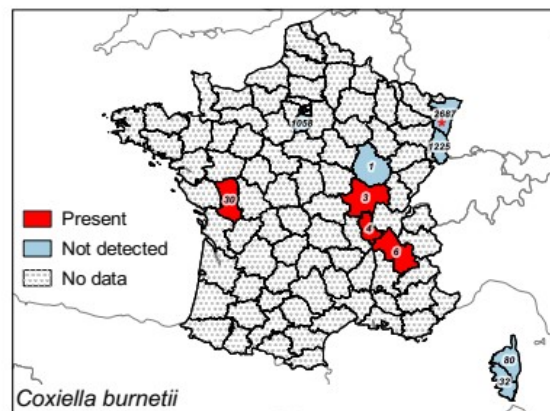
631

632

3.3.5 *Coxiella burnetii* bacterium

633 The bacterium *Coxiella burnetii* is a worldwide pathogen responsible for Q fever (Baca & Paretsky 1983).
634 Potential reservoir host species include ticks, mammals (more than a hundred species recorded) and birds (at
635 least twenty species recorded) (González-Barrio & Ruiz-Fons 2018; Ioannou et al. 2009). However, domestic
636 ruminants are the most frequent reservoir host leading to human transmission (Eldin et al. 2017). The disease
637 causes fever, myalgia, nausea, diarrhea, endocarditis and hepatitis or meningoencephalitis in humans. In
638 ruminants, it is responsible for reproductive disorders and abortions (Agerholm 2013; González-Barrio & Ruiz-
639 Fons 2018; Eldin et al. 2017). DNA of this bacterium has been found in more than 40 hard tick species and in 14
640 soft tick species (Eldin et al. 2017), but vector competence has only been experimentally confirmed for few
641 species (*D. andersoni*, *Haemaphysalis humerosa*, *H. aegyptium*, *H. asiaticum*, *I. holocyclus*, *Ornithodoros*
642 *hermsi*, and *O. moubata*) (Duron et al. 2015). The competence of *I. ricinus* has not been tested, and tick bites
643 are likely not the main transmission route of the bacteria (see in Duron et al. 2015). Indeed, infections can be
644 acquired directly by aerosols from infected vertebrate feces and urine (Eldin et al. 2017) or via the milk of
645 infected female mammals (Pexara, Solomakos & Govaris 2018; Eldin et al. 2016). The bacterium is also
646 excreted in tick feces, which probably contribute to its dissemination in the environment and to infection via
647 aerosol transmission (Körner et al. 2020).

648



649

650 **Figure 6:** Presence map of *Coxiella burnetii* in questing and attached nymph and adult *Ixodes ricinus* ticks in European
651 France by department.

652 Detected presence by PCR methods and respective sampling effort per department in number of tested ticks (nymphs and
653 adults) for *C. burnetii*. * DNA of an unidentified *Coxiella* sp. was detected.

654 In France, few studies have searched for *C. burnetii* in questing *I. ricinus* (**Figure 6; SI 13**). For this bacteria,
655 sequencing is essential to avoid confusion with *Coxiella*-like symbionts (Jourdain et al. 2015). Bonnet et al.
656 (2013) detected DNA of this bacterium in adult ticks from four out of five departments sampled (8 of 44 tested
657 ticks, 18.2%). However, none of 998 questing nymphs, and 60 questing adult ticks from the Paris region
658 (Essonne) were found positive (Lejal et al. 2019a; Lejal et al. 2019b), nor the 62 adults and 3,850 questing
659 nymphs collected in Alsace (Vayssier-Taussat et al. 2013). The 115 *I. ricinus* ticks collected directly on diverse
660 wild and domestic animals in Corsica were all also negative for *C. burnetii* DNA (Grech-Angelini et al. 2020a).

661

662 **3.3.6 The genus *Ehrlichia***

663 Species of the *Ehrlichia* genus are obligate intracellular bacteria that infect mammalian blood cells. Several
664 *Ehrlichia* species are transmitted by ticks and can cause infections in humans and domestic animals (Rar &
665 Golovljova 2011). The known pathogenic species for humans *E. chaffeensis*, *E. ewingii*, *E. minasensis* and
666 *E. ruminantium*, and their known reservoir hosts are cervids, canids and cervids, cattle and cervids, and
667 ruminants respectively. Only *E. canis*, *E. chaffeensis*, *E. minasensis* are known to be present in Europe (Rar &
668 Golovljova 2011; Cicculi et al. 2019). Symptoms in humans are fever, headache, myalgia, and nausea, with only
669 the more severe disease leading to death.

670 The role of *I. ricinus* as vector of these bacteria is still uncertain and requires explicit evaluation. Studies were
671 conducted to search for *Ehrlichia* DNA in questing *I. ricinus* ticks sampled in France, but with mixed results. No
672 positive ticks were found in intensive studies of questing ticks carried out in north-eastern France (Ardennes)
673 (Moutailler et al. 2016b), in the Paris region (Essonne) (Lejal et al. 2019a; Lejal et al. 2019b), and in two sites in
674 north-eastern France (Alsace) (Michelet et al. 2014). Similarly, no positive *I. ricinus* adults were collected from
675 hosts in Corsica (Grech-Angelini et al. 2020a). DNA of the *Ehrlichia* genus was however detected in north-
676 eastern France (Alsace region) in questing *I. ricinus* nymphs and adults, but the species was not identified
677 (Ferquel et al. 2006). Another study in Alsace also found *E. canis* DNA in questing *I. ricinus* nymphs, but the
678 prevalence could not be estimated (Vayssier-Taussat et al. 2013). Strains of *Ehrlichia* bacteria were also
679 detected in western France (Brittany region); one was closely related to a strain from northern Italy, one was very
680 similar to the *Ehrlichia* sp. HI-2000 strain of the *E. canis* group, and the last to a strain identified in Japan
681 (*Ehrlichia* sp. Yamaguchi) and closely related to *E. muris*, which infects rodents (Marumoto et al. 2007). These
682 results suggest a low prevalence of these bacteria in questing *I. ricinus* ticks in France.

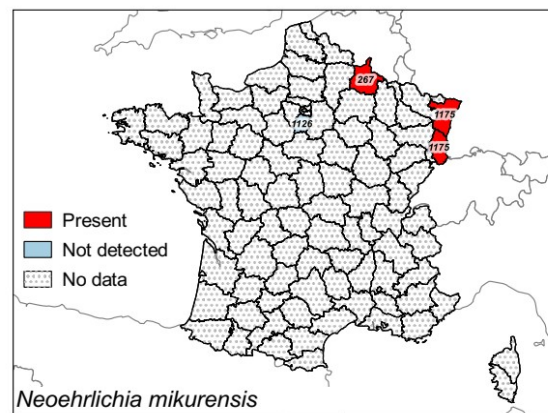
683

684

3.3.5 *Neoehrlichia mikurensis*

685 *Neoehrlichia mikurensis* is an obligatory intracellular bacterium. It was first detected in *I. ricinus* in the
686 Netherlands and *I. ovatus* in Japan, which are – with *I. persulcatus* – likely the main vectors, and in rodents
687 (brown rats, *R. norvegicus*) in China, the reservoir hosts (Schouls et al. 1999; Pan et al. 2003; Kawahara et al.
688 2004). The bacterium was also found in dog blood (Rar & Golovljova 2011). The first human cases of infection by
689 *N. mikurensis* were described in Germany and Sweden in 2007 (von Loewenich et al. 2010; Welinder-Olsson et
690 al. 2010). More recently, the first human cases in France were described (Boyer et al. 2021). This bacterium
691 causes a systemic inflammatory syndrome in persons with hematological or immunological deficiencies,
692 accompanied by fever, diarrhea and other potential complications (Silaghi et al. 2015; Portillo et al. 2018; Wass
693 et al. 2019).

694



695

696 **Figure 7:** Presence map of *Neoehrlichia mikurensis* in questing and attached nymph and adult *Ixodes ricinus* ticks in
697 European France by department.

698 Detected presence by PCR methods and respective sampling effort per department in number of tested ticks (nymphs and
699 adults) for *N. mikurensis*.

700

701 In France, DNA of the bacterium was detected in five out of 276 bank voles from north-eastern France
702 (Ardennes) (Vayssier-Taussat et al. 2012). Questing ticks from the same areas were subsequently tested for
703 infection and 4 out of 267 *I. ricinus* adult females were positive (Moutailler et al. 2016b). Other studies in north-
704 eastern France (Alsace) have reported the presence of the bacterium: 1.7% of questing adult *I. ricinus* (Richter &
705 Matuschka 2012), 1.6% (0.9%-2.5%) of questing nymphs and between 3.2%-6.4% of questing adults of the
706 region (Vayssier-Taussat et al. 2013), and 0.2% (0.02%-0.6%) and 1.3% (0.7%-2.2%) of questing nymphs in

707 Murbach and Wasselone respectively (Michelet et al. 2014). In contrast, no DNA of *N. mikurensis* was found in
708 questing nymphs and adults from the Paris region (Essonne) (Lejal et al. 2019a; Lejal et al. 2019b), nor in
709 Corsica from nine tick species collected from hosts, including 115 *I. ricinus* (Grech-Angelini et al. 2020a). It
710 seems that in France *N. mikurensis* is well present in the north-eastern part (**Figure 7**). Given the limited number
711 of studies to date, additional work will now be required to complete our knowledge of its overall geographical
712 distribution in the country.

713

714 **3.3.6 *Francisella tularensis* and *F. philomiragia* bacteria**

715 *Francisella tularensis* is a facultative intracellular bacterium, present in North-America, Asia and Europe, and
716 detected in several mammal species, mainly lagomorphs and rodents, which are highly susceptible to the
717 bacterium (Larson et al. 2020). It is responsible for tularaemia, a disease characterised in humans by
718 endocarditis, fever, ulcer, pneumonia, septicaemia, myalgia and headache depending on subspecies, site and
719 mode of infection (Hestvik et al. 2014; Gaci et al. 2016). It is suspected to be transmitted by biting insects such
720 as bedbugs, deer flies and ticks and via contact with infected mammals or contaminated water or soil (Genchi et
721 al. 2015; Telford & Goethert 2020).

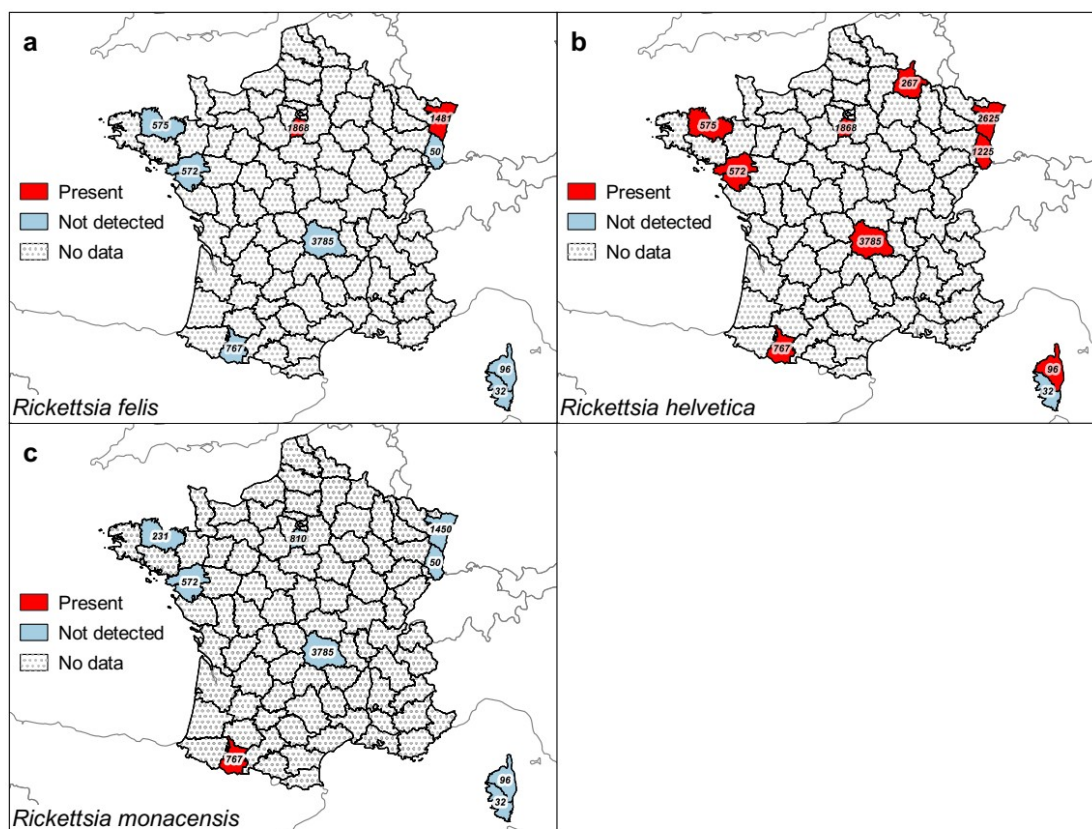
722 The bacterium *F. philomiragia* causes pneumonia, fever and septicaemia in humans (Mailman & Schmidt 2005).
723 Infections with this bacterium are however rare and involve mainly immunodeficient persons or those exposed to
724 contaminated water in their lungs such as after a near drowning experience (Mailman & Schmidt 2005;
725 Kreitmann et al. 2015). Not much is known about the ecology of this bacterium, but it was found in other tick
726 species and possible ecological similarities with the related *F. tularensis* are suspected (Bonnet et al. 2013)

727 In France, studies on the presence of *F. tularensis* and *F. philomiragia* in questing *I. ricinus* ticks are rare
728 (**Figure 8; SI 14**). For this bacteria too, sequencing or specific PCR are necessary to discriminate between
729 *Francisella*-like symbionts and *F. tularensis* (Michelet et al. 2013). DNA of *F. tularensis* was detected in questing
730 ticks sampled in Paris region (Essonne) in two studies, while that of *F. philomiragia* was not (Reis et al. 2011a;
731 Paul et al. 2016). The low prevalence (0-4.3%) in questing adult *I. ricinus* ticks in France is similar to results
732 found in other European countries, and suggests that *I. ricinus* might be only a vector of *F. tularensis* (Reye et al.
733 2013; Sormunen et al. 2021; Egyed et al. 2012; Kirczuk, Piotrowski & Rymaszewska 2021).

734

758 and from north-eastern (Alsace region) France (**Figure 8a**) (Vayssier-Taussat et al. 2013; Lejal et al. 2019a;
759 Lejal et al. 2019), whereas *R. monacensis* DNA was found in southern France (Hautes-Pyrénées; **Figure 8c**)
760 (Akl et al. 2019). Tests to detect DNA of *Rickettsia* SFG were carried out on a large number of questing adult and
761 nymphal ticks in northern-eastern France, but none were found positive (Michelet et al. 2014).

762



763

764 **Figure 9:** Presence maps of *Rickettsia felis*, and *R. helvetica*, and *R. monacensis* in questing and attached nymph and adult
765 *Ixodes ricinus* ticks in European France by department.

766 Detected presence by PCR methods and respective sampling effort per department in number of tested ticks (nymphs and
767 adults) for *R. felis* (a), *R. helvetica* (b), and *R. monacensis* (c).

768

769

3.3.10 The genus *Babesia*

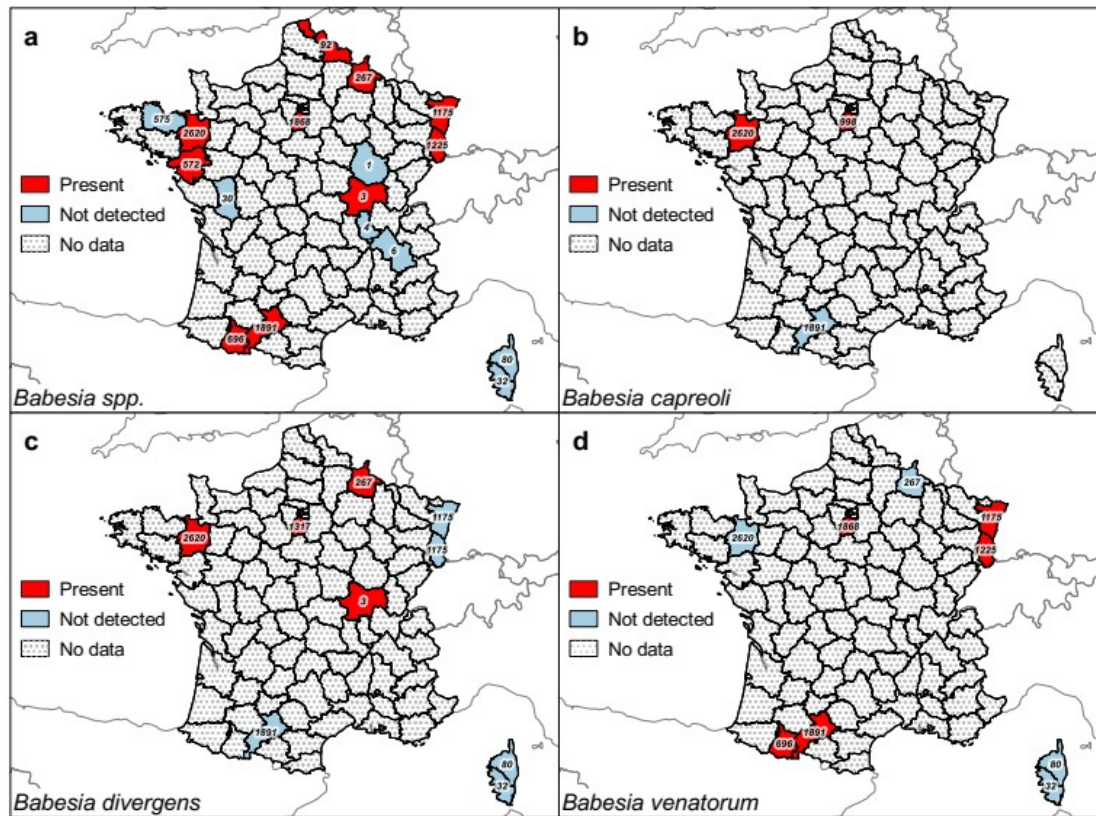
770 *Babesia* sensu stricto belongs to a species-rich genus of unicellular eukaryotes of the Apicomplexa phylum.
771 They are intra-erythrocyte parasites of vertebrates transmitted principally by ticks and generally characterised by
772 transovarian transmission (Walter & Weber 1981; Schnittger et al. 2012; Vannier & Krause 2012; Jalovecka et al.
773 2019). *Babesia* species are responsible for babesiosis, worldwide tick-borne diseases that affect many

774 mammalian species (mainly cattle, sheep, goat, equidae and canids) including humans as accidental hosts
775 (Chauvin et al. 2009). The disease is characterized by hyperthermia, anaemia and haemoglobinuria and can lead
776 to death, particularly in immunosuppressed and splenectomised patients (Hildebrandt et al. 2021). Although tick
777 bites are the main mode of transmission, infections can also occur by blood transfusion (Siński, Welc-Fałęciak &
778 Pogłód 2011; Fang & McCullough 2016). Transmission between dogs has been reported by dog bites for
779 *B. gibsoni* and vertical transmission in dogs is suspected for *B. canis* and *B. vulpes* (formerly *Theileria annae* or
780 “*B. microti*-like”; Baneth et al. 2019) (Solano-Gallego et al. 2016). *Babesia* species responsible for human
781 infection in Europe are mainly *B. divergens* and *B. venatorum*, and exceptionally *B. microti* (Hildebrandt et al.
782 2021). Both *B. divergens*, for which the main reservoir host is cattle, and *B. venatorum* (formerly known as sp.
783 EU1), for which the main reservoir hosts are cervids, are transmitted by *I. ricinus* (see review by Bonnet & Nadal
784 2021). *B. microti*, which infects rodents and shrews, is transmitted by other *Ixodes* species, specific of small
785 mammals such as *I. trianguliceps*. The role of *I. ricinus* in its transmission remains unclear (Walter & Weber
786 1981; Gray et al. 2002; Bown et al. 2008).

787 Several studies have tested for the presence of zoonotic *Babesia* species in questing *I. ricinus* ticks from France
788 (**Figure 9a; SI 16**). *B. divergens* DNA was detected in questing *I. ricinus* ticks from north-eastern (Ardennes), the
789 Paris region (Essonne), central (Saône-et-Loire) and western (Ille-et-Vilaine) France (**Figure 9c**) (Bonnet et al.
790 2013; Moutailler et al. 2016b; Paul et al. 2016; Jouglin et al. 2017b). *B. venatorum* DNA was detected in ticks
791 from the Paris region (Essonne), and the north-eastern (Alsace region), southern (Haute-Garonne), and south-
792 western (Haute-Garonne and Hautes-Pyrénées) regions of the country (**Figure 9d**) (Reis et al. 2011a; Michelet
793 et al. 2014; Paul et al. (2016); Akl et al. 2019; Lejal et al. 2019a; Lejal et al. 2019b; Lebert et al. 2020).
794 Differences in the distribution of the *Babesia* species could be explained by differences in the abundance and
795 prevalence of infection of reservoir hosts in each studied area: *B. venatorum* was more often found in forested
796 landscapes, whereas *B. divergens* occurs in more fragmented landscape with a high proportion of land cover
797 dedicated to cattle breeding.

798 DNA of other *Babesia* species of medical and veterinary interest has also been examined in questing *I. ricinus*:
799 *B. capreoli* that infects cervids (Young et al. 2019); *B. bovis*, *B. bigemina*, *B. major*, *B. occultans* and *B. ovata*
800 which infect mainly cattle; *B. crassa*, *B. motasi* and *B. ovis* which infect mainly goats and sheep; *B. caballi* which
801 infects equines; *B. canis*, *B. gibsoni*, *B. vogeli* and *B. vulpes* which mainly infect canids (Schnittger et al. 2012;
802 Baneth et al. 2015; Solano-Gallego et al. 2016); and *B. microti* (which actually belongs to a separate
803 phylogenetic clade; Schnittger et al. 2012). Among these, only *B. capreoli* was confirmed to be transmitted by

804 *I. ricinus* ticks and its DNA was detected in questing ticks of this species sampled in western France (Ille-et-
805 Vilaine) and in the Paris region (Essonne) (**Figure 9b**) (Jouglin et al. 2017b; Lejal et al. 2019b).
806



807

808 **Figure 9:** Presence maps of all *Babesia* spp., *B. capreoli*, *B. divergens* and *B. venatorum* in questing and attached nymph
809 and adult *Ixodes ricinus* ticks in European France by department.

810 Detected presence maps and respective sampling effort per department in number of tested ticks (nymphs and adults) for
811 *Babesia* spp. (a), *B. capreoli* (b), *B. divergens* (c) and *B. venatorum* (d).

812

813 3.3.11 The genus *Theileria*

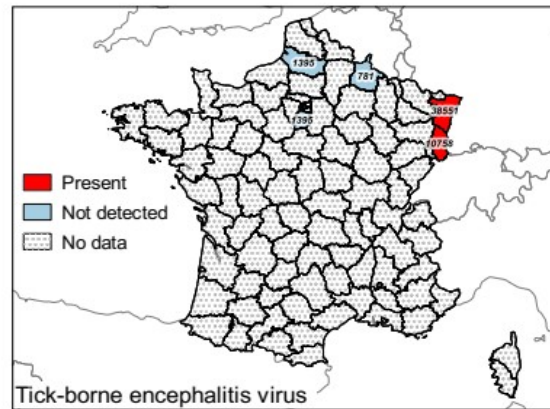
814 Although closely related, parasites from the *Theileria* genus differ from those of *Babesia* by a pre-erythrocyte
815 stage in lymphocytes in the vertebrate host, and by the absence of transovarian transmission in the tick vector
816 (Mans, Pienaar & Latif 2015). These parasites infect mainly ruminants in countries from the southern
817 Hemisphere, where they are responsible for important economic loss (Mans, Pienaar & Latif 2015), and horses
818 (*Theileria equi*) worldwide (Nadal, Bonnet & Marsot 2021). Parasites belonging to this genus are not known to
819 infect humans.

820 In several studies, *I. ricinus* ticks sampled in France were examined for the presence of DNA from several
821 *Theileria* species that are known to occur in Europe and around the Mediterranean basin (**SI 16**); none was
822 detected. However, strains closely related to *T. parva* and *T. taurotragi* were found by high-throughput
823 sequencing methods in questing *I. ricinus* nymphs sampled in north-eastern France (Alsace region), but no
824 prevalence estimates were calculated (Bonnet et al. 2014). Interestingly, *T. equi* DNA was detected in adult
825 *I. ricinus* that were questing or attached to piroplasm-free vertebrate hosts in Spain, Italy and the Netherlands
826 (Butler et al. 2016; Garcia-Sanmartin et al 2008; Iori et al. 2010). These results highlight the need to study the
827 vector competence of *I. ricinus* for *T. equi* and other *Theileria* species present in Europe to evaluate its potential
828 contribution in the transmission of the pathogen to horses.

829

830 **3.3.12 Tick-borne encephalitis virus**

831 Tick-borne encephalitis (TBE) was described for the first time in 1931 in Austria and the virus (TBEV) was
832 isolated in 1937 in Russia (see review by Kaiser 2008 and Zlobin, Pogodina & Kahl 2017). This virus belongs to
833 the *Flavivirus* genus of the Flaviviridae family (simple stranded RNA virus). Three main virus sub-types have
834 been identified: the “European” sub-type, the “Far-Eastern” sub-type, and the “Siberian” sub-type. However, two
835 other subtypes have been recently described: the Balkanian and the Himalayan sub-types (Ruzek et al. 2019).
836 The main reservoir hosts are small mammals, among which *Apodemus* spp. mice seem to be particularly
837 infectious for ticks (Labuda et al. 1993c; Labuda et al. 1996; Labuda et al. 1997; Knap et al. 2012). The virus
838 causes meningitis and meningoencephalitis in humans, which can lead to neurological sequelae, such as
839 paralysis, and death. The Far-Eastern subtype results in the most severe forms of the disease, with death in up
840 to 2% of patients (Ruzek et al. 2019). TBEV is mainly transmitted by *I. ricinus* and *I. persulcatus* ticks in Europe
841 (Mansfield et al. 2009). Human infections can occur not only by tick bites, but also by consumption of
842 unpasteurised milk or dairy products from infected animals (Süss 2011). Transovarian transmission in ticks is
843 weak (Danielova et al. 2002; Labuda et al. 1993a), but co-feeding transmission, where an infected tick infects
844 non-infected ticks feeding nearby on the host, is of greater epidemiological importance (Labuda et al. 1993c;
845 Labuda et al. 1997). Indeed, it was established that co-feeding transmission is of paramount importance in
846 maintaining the virus in tick populations and thus its circulation in vertebrate hosts (Randolph, Gern & Nuttal
847 1996).



848

849 **Figure 10:** Presence map of tick-borne encephalitis virus (TBEV) in questing and attached nymph and adult *Ixodes ricinus*
850 ticks in European France by department.
851 Detected presence of TBEV by RT-PCR methods and sampling effort per department in number of tested ticks (nymphs and
852 adults).

853

854 Only the “European” sub-type, considered as the least virulent, is present in western Europe (Bestehorn et al.
855 2018). In France, TBEV prevalence in questing *I. ricinus* ticks seems low (<0.1% in larvae and <1% in nymphs
856 and adults) and is probably localised in micro-foci (Chatelain & Ardouin 1978; Pérez-Eid, Hannoun & Rodhain
857 1992; Bournez et al. 2020a). Too few studies have been conducted to conclude on the distribution of TBEV and
858 its spatio-temporal variation in questing ticks in France, but it is likely present throughout the north-eastern part
859 of the country, with well-identified endemic foci in the Alsace region (**Figure 10; SI 17**) (Pérez-Eid, Hannoun &
860 Rodhain 1992; Hansmann et al. 2006; Rigaud et al. 2016; Bournez et al. 2020a). Serological results from wild
861 ungulates suggest that the virus is also likely circulating in northern, north-eastern and eastern France, and that
862 a closely related virus is present in the Pyrenees (Bournez et al. 2020b). Human TBE cases have been reported
863 in western and central France (Rhône-Alpes and in Auvergne regions) during the last decade (Velay et al. 2018;
864 Botelho-Nevers et al. 2019). In 2020, 43 TBE cases occurred in eastern France (Ain) following the consumption
865 of goat cheese made with contaminated raw milk and thus identified a new focus (Beaufils et al. 2021; Gonzalez
866 et al. 2022). The distribution of the virus seems to be changing in Europe, probably because of global changes
867 that affect larvae and nymph co-occurrence on hosts and thus the probability of co-feeding transmission.
868 However, this trend might be biased by a better detection of human cases and other socio-economical changes
869 (Randolph et al. 2000; Randolph & Rogers 2000). Since 2021, TBE has been listed as a reportable disease in
870 France, a measure that should improve our knowledge on human exposure.

871 **3.3.13 Other viruses**

872 The Eyach virus is a *Coltivirus* that could be responsible for neurological damage, as seropositivity was
873 associated with neuropathies in areas of the former Czechoslovakia (Malkova et al. 1980; Charrel et al. 2004).
874 The virus was first isolated in Germany in 1972 from *I. ricinus* ticks and then again in western France in 1981
875 (Mayenne) from *I. ricinus* and *I. ventalloi* ticks collected from a European rabbit (Rehse-Küpper et al. 1976;
876 Chastel et al. 1984). However, the vector competence of *I. ricinus* for this virus has not been formally
877 demonstrated and the role of the European rabbit as reservoir remains unclear (Chastel 1998; Charrel et al.
878 2004). More recently, viral RNA was detected in questing *I. ricinus* ticks in north-eastern France; in the Alsace
879 region in 2010 and in the Ardennes department in 2012 (Moutailler et al. 2016a).

880

881 **4 Conclusions**

882 This systematic map and narrative review assembled results of studies published in European France between
883 1965 and 2020 at various spatial scales (country-wide to site-specific) and exploring the influence of different
884 variables (meteorological, biogeographic zones, landscape features, host density, local vegetation, soil
885 characteristics) on the density of questing *I. ricinus*. It also provided summary information on the prevalence and
886 distribution of several tick-borne pathogens detected in *I. ricinus* ticks in the country.

887 The first studies on the distribution of ixodid tick species in France started in the 60's (Lamontellerie 1965; Panas
888 et al. 1976). Gilot and colleagues then started to examine the association of *I. ricinus* with different vegetation
889 types and its related phenology (Gilot, Pautou & Mancada 1975; Gilot et al. 1975). After that, more standardised
890 studies on the distribution and phenology of the species were performed (e.g., Gilot et al. 1989; Gilot et al.
891 1994). More recent work has focused on identifying landscape, vegetation and microclimatic factors associated
892 with the abundance and phenology of the species using standardised methods and new technologies (e.g., via
893 Geographic Information Systems). The advent of PCR technologies also enabled researchers to examine the
894 present of associated pathogens. These different studies have thus made it possible to accumulate a certain
895 amount of knowledge about *I. ricinus* in France, but no synthesis of these data was available. This study aimed
896 to fill this void and to highlight remaining knowledge gaps on the distribution, phenology, and host range of
897 *I. ricinus* and on the prevalence of its associated pathogens in certain regions of France.

898 For example, larval phenology is still poorly described overall, and larval-nymphal phenology and host use under
899 Mediterranean climates remain to be investigated. More longitudinal studies on *I. ricinus* phenology that include

900 multiple environmental parameters are also necessary to better define factors essential for the development of
901 the species and to predict acarological risk, particularly in a context of climate change. Very few such studies
902 have been conducted in France so far (Paul et al. 2016; Wongnak et al. 2022).

903 Studies on tick host use has focused mainly on Rodentia (mice and voles) and wild Cetartiodactyla (e.g., roe
904 deer), whereas the role of domestic Cetartiodactyla (cattle, sheep, and goats), Perissodactyla (horses and
905 donkey), Carnivora (e.g. cats, dogs, foxes), Aves (birds), Eulipotyphla (shrews and hedgehogs), Lagomorpha
906 (e.g., rabbits and hares), and Squamata (e.g. lizards and snakes) remain poorly quantified. It should also be
907 noted that the few studies that exist are rarely comparable (different location, season and/or protocol),
908 preventing direct comparisons of tick burdens between species or between different climates or environments for
909 a same species. A standardisation of protocols is thus called for.

910 Studies of tick-borne pathogens have focused mainly on *B. burgdorferi* s.l. In addition, due to logistical
911 constraints, these studies have often concentrated around locations of the investigating research units and, more
912 distant or isolated regions have therefore received less attention, leading to a lack of data to inform and prevent
913 tick-borne disease in some local populations (Septfons et al. 2018). This highlights the need to scale studies
914 according to expected outcomes, to ensure for instance that the targeted area lies within the expected domain of
915 the desired model. That said, the data available on *B. burgdorferi* s.l. were sufficient to compare prevalence and
916 the occurrence of different genospecies in questing ticks among regions. The observed gradients mirror
917 observations at the European scale: an increasing prevalence along a SW-NE gradient with an increasing
918 proportion of prevalence of *B. afzelii* (Strnad et al. 2017). These prevalence gradients are likely driven by
919 biogeographic gradients in Europe and the evolutionary history of *Borrelia* genospecies (Margos et al. 2011).
920 The distribution and the spatial variation in prevalence of other tick-borne pathogens are still poorly known and
921 deserve further study. Due to the veterinary importance of babesiosis, the fact that several species can infect
922 humans, the numerous side effects of babesicidal drugs, and the absence of a vaccine against most of the
923 species that occur in France (only a vaccine against *B. canis* exists, to our knowledge: Pirodog, Boehringer
924 Ingelheim Animal Health, France), it is particularly important to intensify research and monitoring of these
925 parasites. Likewise, recent distributional changes in TBEV exposure should be more closely tracked to anticipate
926 prevention. For example, understanding the potential role of birds as dispersers of infected ticks for the
927 geographic expansion of the virus would be extremely informative (Wilhelmsson et al. 2020).

928 Detection methods of infectious agents in ticks have rapidly improved over the last decades, particularly with the
929 development of high throughput sequencing methods and more sensitive PCR techniques (i.e., quantitative

930 PCR, microfluidic PCR, digital PCR). That said, it is important to remember that the detection of pathogen DNA
931 in an arthropod does not imply that the arthropod is a vector of this organism, it only indicates that a blood meal
932 was taken on an infected host. The formal demonstration of vector competence requires experimental study
933 (Khal et al. 2002; Bonnet & Nadal 2021). Although the vector competence of *I. ricinus* has been experimentally
934 demonstrated for many important infectious agents, its role in the transmission of other agents such as
935 *C. burnetii*, *F. tularensis*, *F. philomiragia*, and *Rickettsia* spp. still requires experimental validation. Reciprocally,
936 other species can be the vectors of some pathogens transmitted by *I. ricinus* and their role in the zoonotic cycle
937 requires explicit consideration. For instance, few tick species have been experimentally assessed for vector
938 competence for *B. burgdorferi* s.l. (Eisen 2020), although these bacteria have been frequently detected in
939 *I. acuminatus* (Doby et al. 1990; Szekeres et al. 2015), *I. arboricola* (Spitalska et al. 2011; Heylen et al. 2013),
940 *I. frontalis* (Heylen et al. 2013; Heylen et al. 2017a; Heylen et al. 2017b; Palomar et al. 2017), *I. hexagonus*
941 (Gern et al. 1991; Geurden et al. 2018) and *I. trianguliceps* (Doby et al. 1990; Nefedova et al. 2005). Knowledge
942 on vector diversity and the relative roles of different vector species is essential for understanding the distribution
943 and observed variation in pathogen prevalence and to establish pertinent prevention measures. The role of other
944 co-infecting tick microorganisms, symbiotic or commensal, in the ecology, physiology and vector competence of
945 *I. ricinus* also needs to be investigated (Bonnet & Pollet 2021; Lejal et al. 2021). Such studies could uncover new
946 ways of controlling ticks and the pathogens they transmit.

947 To conclude, more studies are needed to better assess the distribution of *I. ricinus* and its associated pathogens
948 in France, particularly in the context of current global changes that could see a shift in the distribution of native
949 species, the emergence of tropical species in Europe and changes in tick phenology and transmission dynamics.
950 Efforts focused on a better understanding of tick-borne pathogen ecology is also necessary to better evaluate
951 acarological risk. Indeed, human cases of Lyme borreliosis have increased over the last two decades for diverse
952 reasons (e.g., awareness of clinicians, increasing outdoor recreational activities, modifications of the tick
953 ecosystems, etc.) and new tick-borne diseases have emerged like relapsing fever associated with *B. miyamotoi*
954 or *N. mikurensis* (Figoni et al. 2019). Current participative science projects like CITIQUE (<https://www.citique.fr/>),
955 based on voluntary declarations of tick-bites and tick collection, may fulfil some of these gaps in the future. For
956 example, data collected under these programs should help complete the distribution map of *I. ricinus* and its
957 associated pathogens and should provide information on high human exposure periods (Eisen & Eisen 2021).
958 More generally, an integrated research programme that links data and knowledge from diverse sources would
959 help to develop more efficient strategies to control tick populations and reduce tick-borne disease risk.

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965

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972

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974 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the
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976

977 **Data and code availability**

978 All encoded and compiled data are available as supplementary information at
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980

981 **Authors' contributions**

982 GP and SB designed the study. GP conducted the literature search, screened the references, developed the
983 bibliographic database and compiled all the data, wrote the first draft of the manuscript and produced all figures
984 and tables. BL gave valuable methodological recommendations. LB, NB, KDM, JF, BL, EQ, MRM and SB
985 discussed data interpretation and presentation and edited the manuscript, figures and tables.

986

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