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# 1 Seasonality of host-seeking *Ixodes ricinus* nymph abundance in relation to 2 climate

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23

## 24 Abstract

25 There is growing concern about climate change and its impact on human health. Specifically, global  
26 warming could increase the probability of emerging infectious diseases, notably because of changes in  
27 the geographical and seasonal distributions of disease vectors such as mosquitoes and ticks. For  
28 example, the range of *Ixodes ricinus*, the most common and widespread tick species in Europe, is  
29 currently expanding northward and at higher altitudes. However, little is known about the seasonal  
30 variation in tick abundance in different climates. Seasonality of *I. ricinus* is often based on expert  
31 opinions while field surveys are usually limited in time. Our objective was to describe seasonal  
32 variations in *I. ricinus* abundance under different climates. To this end, a seven-year longitudinal study,  
33 with monthly collections of *I. ricinus* host-seeking nymphs, was carried out in France, in six locations  
34 corresponding to different climates. Tick data were log-transformed and grouped between years so as

35 to obtain seasonal variations for a typical year. Daily average temperature was measured during the  
36 study period. Seasonal patterns of nymph abundance were established for the six different locations  
37 using linear harmonic regression. Model parameters were estimated separately for each location.  
38 Seasonal patterns appeared different depending on the climate considered. Western temperate sites  
39 showed an early spring peak, a summer minimum and a moderate autumn and winter abundance.  
40 More continental sites showed a later peak in spring, and a minimum in winter. The peak occurred in  
41 summer for the mountainous site, with an absence of ticks in winter. In all cases except the  
42 mountainous site, the timing of the spring peak could be related to the sum of degree days since the  
43 beginning of the year. Winter abundance was positively correlated to the corresponding temperature.  
44 Our results highlight clear patterns in the different sites corresponding to different climates, which  
45 allow further forecast of tick seasonality under changing climate conditions.

46

47

## 48 **Introduction**

49

50 The effect of human activity on climate change is now recognised (IPCC, 2021, even though the extent  
51 of its impact remains open to debate. In particular, the influence of anthropogenic climate change on  
52 infectious disease incidence has to be assessed. Among infectious diseases, vector-borne diseases  
53 appear to be especially sensitive to climate change (Semenza and Suk, 2018) because changes in  
54 temperature and rainfall regime inevitably affect vector spatial distribution and phenology. However,  
55 climate change does not represent the unique disruptor of vector borne diseases (Rocklöv and  
56 Dubrow, 2020), which can also be impacted by biodiversity loss and land use change (Rizzoli et al.,  
57 2019).

58 Climate change may greatly affect the distribution of ticks, which are the main vectors of zoonotic  
59 pathogens in Europe (Gray et al., 2009; Ogden and Lindsay, 2016). Temperature influences tick  
60 physiology through the process of development, which is known to be accelerated with higher  
61 temperatures (Randolph et al., 2002). Tick host-seeking activity (referred to as “questing” for most tick  
62 species) also increases with temperature and relative humidity (Vail and Smith, 1998; Perret et al.,  
63 2003). Tick survival could, on the contrary, be reduced by higher temperatures and especially lower  
64 hygrometry (Daniel et al., 1976). The impact of climate change on tick distribution has already been  
65 observed and reported with a trend towards a northward expansion of *Ixodes ricinus* in Europe  
66 (Lindgren et al., 2000) or its occurrence at higher altitude (Daniel et al., 2003). These conclusions were  
67 directly drawn from tick collections, but the shift in latitude and altitude could also be assessed thanks  
68 to indirect observations. For instance, prevalence of antibodies against *Anaplasma phagocytophilum*  
69 in sheep can be used to estimate the frequency of bites from *I. ricinus* (Jore et al., 2014). Lindgren and  
70 Gustafson (2001) related an increase in Tick-Borne Encephalitis cases to milder winters and earlier  
71 springs.

72 Data on tick occurrence and climate variables have been confronted to define climate suitability for  
73 ticks such as *I. ricinus* (Estrada-Peña and Venzal, 2006). Extrapolation to future climate projections  
74 were then derived from these suitability maps (Estrada-Peña et al., 2012; Poretta et al., 2013). Besides  
75 these statistical models, mechanistic models incorporating knowledge on biological processes were  
76 also developed, for instance for *Hyalomma marginatum* (Estrada-Peña et al., 2011) or *I. ricinus* (Hoch  
77 et al., 2010). These process-based models could allow the simulation of the impact of climate change  
78 through the effect of meteorological variables on the involved processes. They represent relevant tools  
79 to predict the evolution of the transmission of tick-borne pathogens such as Crimean Congo  
80 Haemorrhagic Fever Virus (CCHFV) (Estrada-Peña et al., 2013; Hoch et al., 2018) or Lyme disease  
81 agents, for which the northward expansion has been simulated in North America (Ogden et al., 2008).  
82 More recently, Li et al. (2016) developed a mechanistic agent-based model to simulate the seasonality

83 of Lyme disease risk, estimated through the number of infected nymphs in Scotland. Their model  
84 predicts an increase in disease risk at higher latitude and altitude, but also in the duration of *I. ricinus*  
85 host-seeking season, with warmer conditions. Such a longer duration of the host-seeking season has  
86 also been predicted by the model developed by Hancock et al. (2011), which focused on the evolution  
87 of the timing of *I. ricinus* peak of abundance in response to increasing temperature. Processes affecting  
88 the phenology of *Ixodes scapularis* were identified by a study linking simulation and data collection in  
89 different sites of the United States (Ogden et al., 2018). These authors identified different observed  
90 patterns of tick abundance depending on the site. They carried out several simulations considering  
91 different scenarios regarding temperature-independent diapause and development. The comparison  
92 of simulation outputs with observations suggested that diapause may be a major factor to explain  
93 geographical differences in tick phenology.

94 The objective of our study was to assess the differences in seasonal patterns of *I. ricinus* nymphal  
95 abundance associated with distinct climates observed in France. A seven-year longitudinal study,  
96 involving monthly *I. ricinus* collections, was carried out at six locations in France. The species *I. ricinus*  
97 was targeted because it is responsible for major human vector-borne diseases in Europe (Lyme  
98 borreliosis and Tick Borne Encephalitis). This dataset allowed the fitting of statistical models of nymph  
99 abundance with time. Wrongnak et al. (2022a) fitted a model on the same data set to explore the  
100 influence of meteorological variables on tick abundance for predictive purposes. Our modelling  
101 approach is complementary and aims to describe the seasonal patterns of *I. ricinus* by site and to relate  
102 them to temperature features of the different geographical locations. This approach can give insight  
103 into the evolution of tick phenology in relation to climate change.

104

## 105 **Data and models**

106

### 107 *Tick sampling*

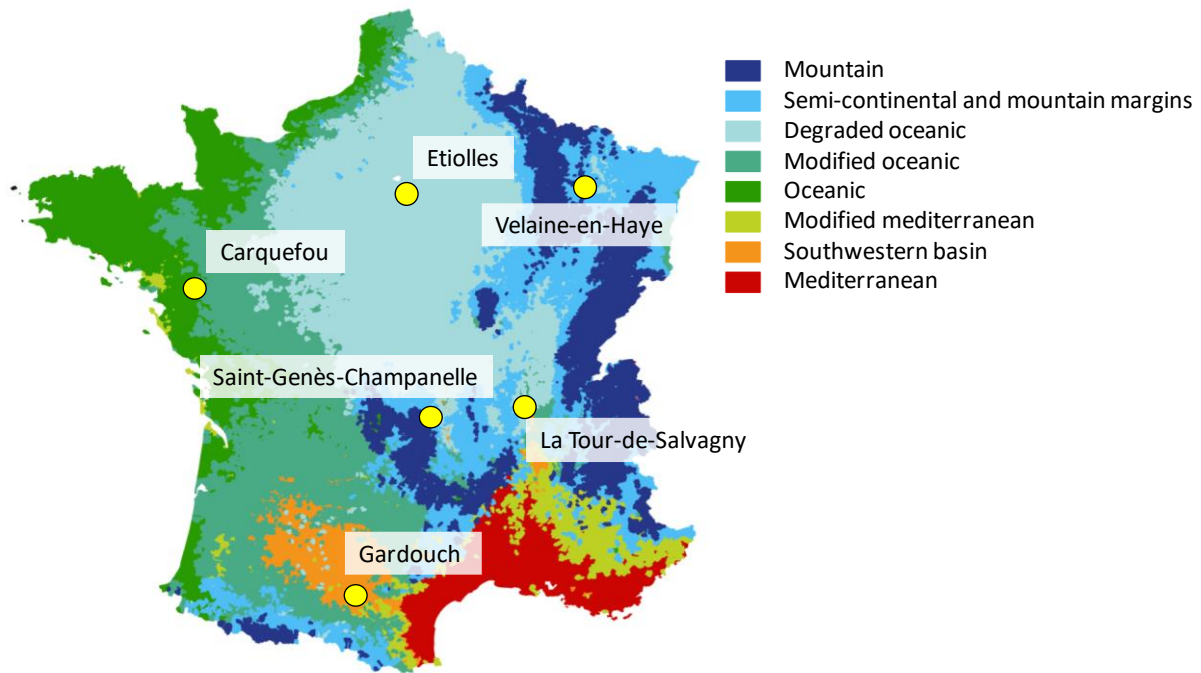
108

109 Tick collection was carried out between April 2014 and June 2021 at six locations across France (Figure  
110 1) which will be thereafter called Carquefou, Etiolles, Gardouch, La-Tour-de-Salvagny, Saint-Genes-  
111 Champanelle and Velaine-en-Haye. These locations were chosen in wooden habitats, selected for their  
112 high densities of host-seeking *I. ricinus* nymphs during spring, in different regions of France  
113 characterized by different climates (see Table S1, Supplementary Material, for GPS coordinates of the  
114 locations, altitudes and corresponding climates). In Gardouch, two nearby sites were sampled over the  
115 entire period: "Gardouch-in", an enclosed forest patch with a controlled population of roe deer, and  
116 "Gardouch-out", another part of the same forest, just outside the fence of "Gardouch-in" and with  
117 uncontrolled roe deer populations. In La Tour-de-Salvagny, a first site (called " La Tour-de-Salvagny a"

118 thereafter) was sampled between April 2014 and September 2016, then became inaccessible and was  
119 replaced by a second site (called " La Tour-de-Salvagny b" thereafter, approximately 2 km apart),  
120 sampled between April 2017 and June 2021. There was therefore a total of eight sites at six locations.  
121 Time-series of tick counts were obtained through 520 field campaigns carried out from April 2014 to  
122 June 2021, corresponding approximately to one collection session per month and per site (some  
123 months are lacking due to external constraints: snow, Covid-19 lockdown...).

124 At each site, ten marked transects of 10 x 1 m long were chosen along trails covered by short grass or  
125 a leaf litter, with a minimum distance of 20 m between them. Each tick collection session corresponded  
126 to a single day, selected for the absence of rain or snow and the dryness of the grass and leaf litter  
127 cover. On that day, on each transect, a 1 m<sup>2</sup> white flannel was slowly dragged along the 10 m to collect  
128 host-seeking ticks (Agoulon et al., 2012): ticks were counted, removed from the cloth with tweezers  
129 and stored alive for further identification at stage and species level according to identification keys  
130 (Pérez-Eid, 2007). Tick collection was repeated three times consecutively on the same marked  
131 transects in order to collect more individuals and to improve accuracy in the assessment of tick  
132 abundance (Bord et al., 2014). This method simulates the natural detection and infestation of a host  
133 by host-seeking ticks. The number of collected ticks was therefore considered representative of the  
134 host-seeking tick abundance on the day of collection. Due to a low number of adult ticks collected and  
135 the known low involvement of larvae in disease transmission cycle, these development stages were  
136 not considered for further analyses: only *I. ricinus* nymphs were considered, reflecting the major risk  
137 of pathogen transmission to humans (Kurtenbach et al., 2006).

138



139

140 Figure 1: Map of France with the different climates encountered (from Joly et al., 2010). Tick sampling  
141 locations are indicated

142

#### 143 *Local temperature*

144

145 Weather stations were installed at the beginning of the period at each location to collect hourly air  
146 temperature records at a height of 1.5 meters. A single station was used for La Tour-de-Salvagny a and  
147 b, and for Gardouch-in and Gardouch-out. Daily mean temperatures were obtained from those  
148 records. When data were missing, data from nearby MétéoFrance and INRAE automatic weather  
149 stations were collected to impute the missing values, with a random forest approach (Wongnak et al,  
150 2021). For each location, the daily mean temperatures of an average year were obtained by averaging  
151 the daily mean temperatures from 1 January to 31 December (see Figure S1, Supplementary Material).  
152 In order to assess the influence of temperature on the date of the estimated peak, a cumulative  
153 temperature (in degree-day) was computed for each location. It was calculated by summing the daily  
154 mean temperatures of an average year from the 1<sup>st</sup> January up to the estimated date of the peak.

155

#### 156 *Statistical analyses*

157

158 The objective of the analyses was to describe the site-specific seasonal variations in the abundance of  
159 *I. ricinus* nymphs, hereafter referred to as tick abundance pattern. The distributions of the numbers of  
160 nymphs for each site were right skewed, typically with a mode below 10 nymphs collected per day and

161 maximum values that could reach several hundred. Taking the natural logarithm of the number of  
162 nymphs allowed to make the distributions more symmetrical (see figure S2, Supplementary Material).  
163 The abundance patterns were modelled using harmonic regressions. Briefly, harmonic regression is a  
164 type of linear regression in which the days of the year are mapped onto a circle, and, functions of the  
165 sine and cosine of the corresponding angles are included as covariates in the regression.  
166 The outcome of all models was the natural logarithm of the number of *I. ricinus* nymphs (+1 to avoid  
167  $\ln(0)$ , which is not defined) collected at a given site on a given day. This outcome was modelled as a  
168 function of day of the year at the time of collection. The models' specifications were as follows:

$$169 \quad \ln(y_{st} + 1) = \mu_s + \sum_{k=1}^K \left( a_k \cos\left(k \frac{2\pi d}{365}\right) + b_k \sin\left(k \frac{2\pi d}{365}\right) \right) + \varepsilon_{st}$$

170

171 with:

$$172 \quad \varepsilon_{st} \sim \mathcal{N}(0, \sigma^2)$$

173

174 Where  $y_{st}$  was the number of nymphs collected at site  $s$  on day of year  $d$ ;  $\mu_s$  was the model intercept  
175 for site  $s$ ,  $K$  was the maximum number of periodic (also called Fourier) terms included; and  $\varepsilon_{st}$  was the  
176 residual error with mean 0 and variance  $\sigma^2$ .

177 Increasing  $K$  makes it possible to model increasingly complex seasonal patterns. In order to mitigate  
178 the risk of overfitting with high values of  $K$ , models with  $K$  varying between 0 and 4 were compared  
179 based on the Akaike Information Criterion (AIC) value. For most locations, there was an important  
180 decrease in AIC between  $K = 0$  and  $K = 2$  (see Figure S3, Supplementary Material), and the decrease  
181 was less pronounced between  $K = 2$  and greater values for  $K$ . Therefore,  $K = 2$  was used in all models.  
182 Using the fitted models, typical within-year evolutions of tick abundance were simulated. The  
183 characteristics of interest included the date of peak abundance, i.e. the date when the predicted  
184 number of *I. ricinus* was highest. The relation of the peak dates with cumulative mean temperatures  
185 were investigated.

186 Furthermore, to analyse the potential links between temperature and winter tick activity, the average  
187 January mean temperature was compared to the corresponding estimated mean tick abundance. To  
188 improve comparability among sites, average tick abundance in January was standardized by its  
189 maximum value in each site.

190

## 191 **Results**

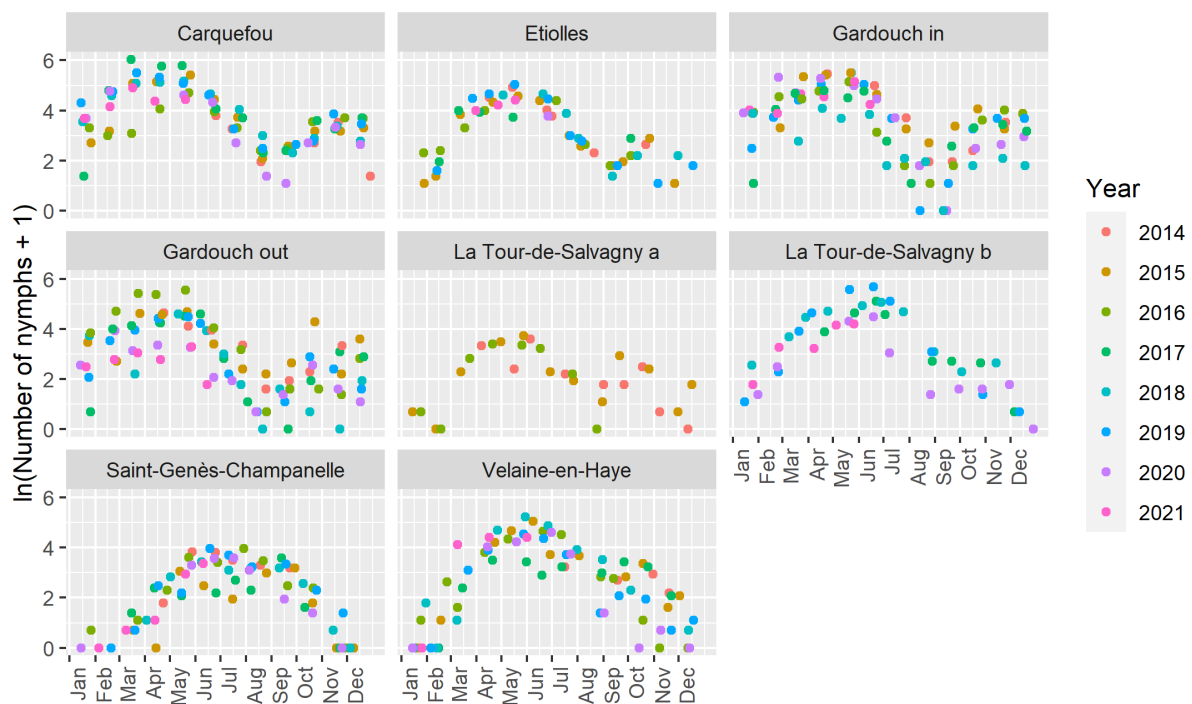
192

193 *Seasonal patterns of observed I. ricinus nymphal abundance at the different sites*



194

195 Figure 2 shows the natural logarithm of the number of *I. ricinus* nymphs (+1) collected as a function of  
196 the day of the year, for the eight sites and seven years of collection. At a given site, seasonal patterns  
197 were stable over years, whereas there were variations among sites exhibiting different patterns.  
198 Therefore, we fitted different models for the different locations, including data from all years for each  
199 site. When there were two sites for the same location (*i.e.* Gardouch in and out, La Tour-de-Salvagny  
200 a and b), the patterns looked similar. In those cases, we included site as a fixed effect in the harmonic  
201 regression (different mean for each site), but the same coefficients were used for the Fourier terms:  
202 this means that the fitted curves followed the same seasonal dynamics but were of different heights.  
203



204

205 Figure 2: Natural logarithm of the observed number of *Ixodes ricinus* nymphs (+1) collected as a  
206 function of day of the year, at eight French sites over seven years.

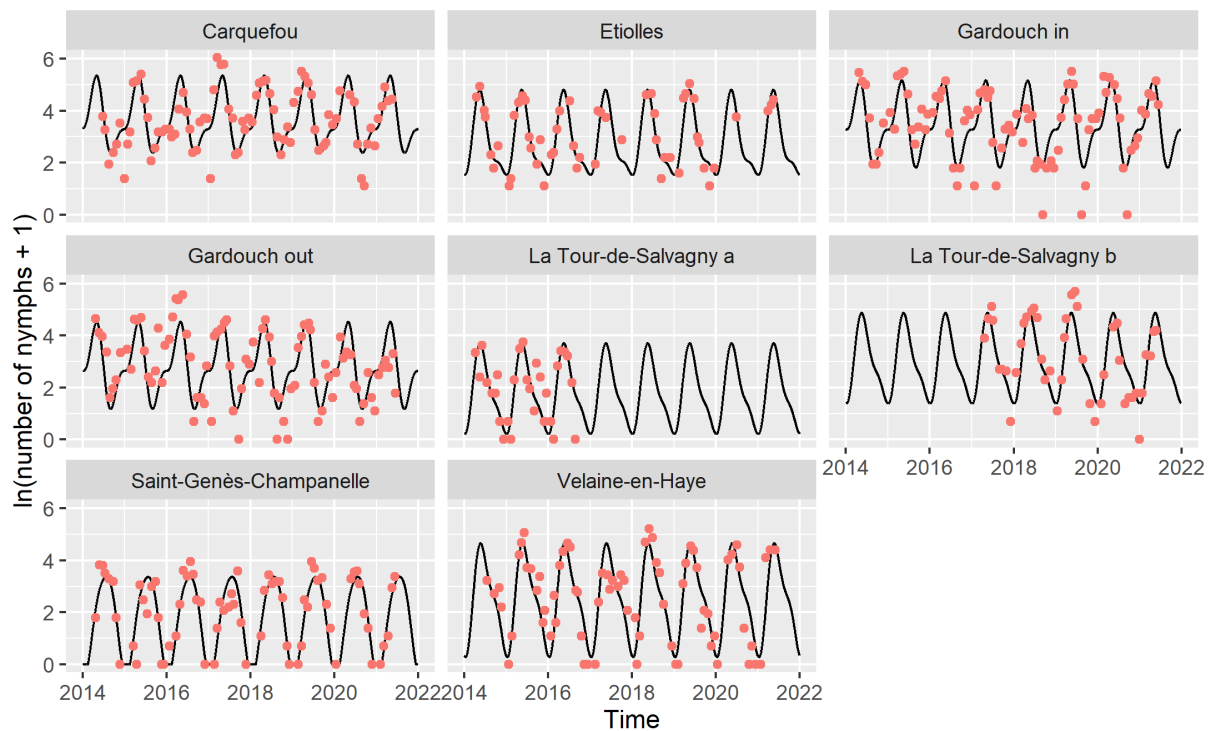
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208 *Seasonal patterns of fitted I. ricinus nymphal abundance at the different sites*

209

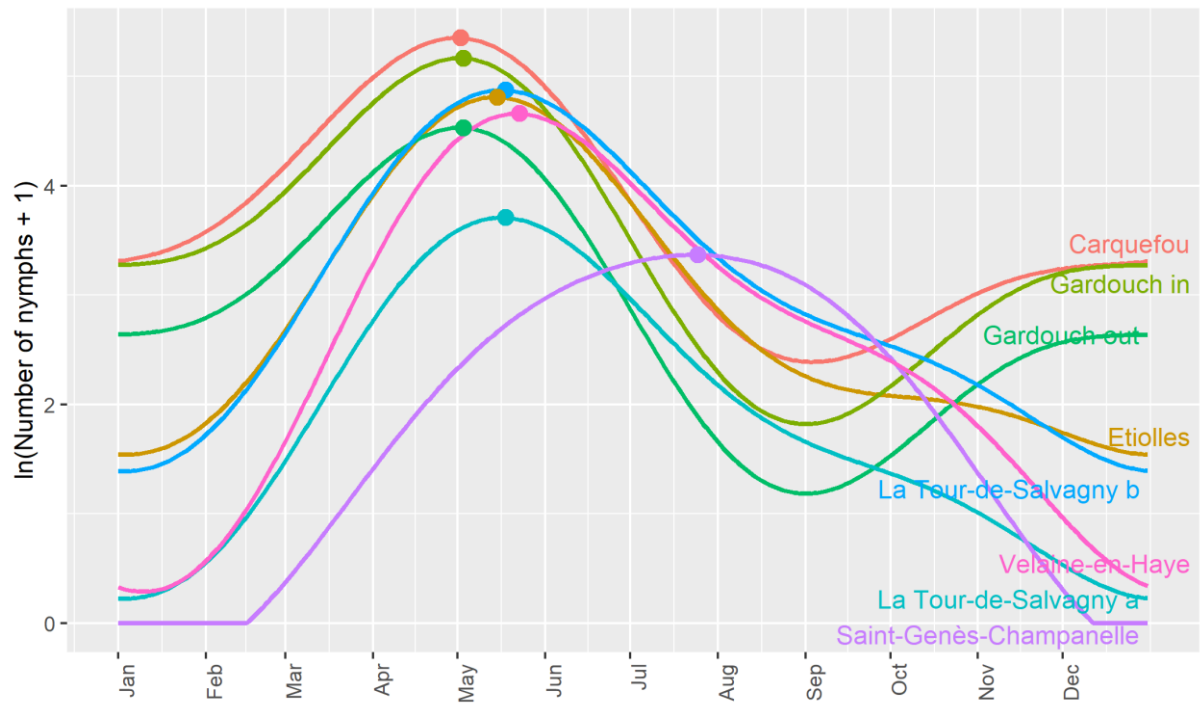
210 The different models appear to correctly represent the observed dynamics (Figure 3) and particularly  
211 the spring peak. For Gardouch-in and Gardouch-out as well as for the two sites of La Tour-de-Salvagny,  
212 the choice of fitting the same model with a distinct intercept seems relevant. In particular, for the  
213 latter, the model succeeds in representing both the same dynamics and the difference in abundance  
214 between the two sites. When applied over the whole data set without accounting for the sampling

215 year, such a modelling helps to identify the favourable and less favourable years for tick abundance,  
216 for which observed tick abundances are respectively above and below the fitted curve. Interestingly,  
217 favourable years seem to differ from one site to another, even on the same location (Gardouch in and  
218 out). For instance, the model revealed a favourable year in 2016 at Gardouch out (but not at Gardouch  
219 in), in 2017 at Carquefou, in 2018 at Velaine-en-Haye and in 2019 at La Tour-de-Salvagny (b).  
220



221  
222 Figure 3: Natural logarithm of the number of *Ixodes ricinus* nymphs (+1) predicted by the models (black  
223 curves) and number of nymphs effectively collected (red dots), at eight French sites over seven years.

224  
225 To compare sites, we superimposed the predicted tick abundance for all sites over one year (Figure 4).  
226 The predicted patterns show a spring peak in all sites except Saint-Genès-Champanelle, where the  
227 maximal abundance is observed in summer. Some small differences in spring peak dates are predicted  
228 for the other sites. Tick peak occurs earlier for the western “oceanic” sites (Carquefou and Gardouch)  
229 and later for the eastern “continental” sites (Etiolles, La Tour-de-Salvagny and then Velaine-en-Haye).  
230 Winter abundance highlights another striking feature: in the western sites (Carquefou and Gardouch),  
231 predicted tick abundance is increasing from September to November to reach a plateau throughout  
232 the winter months, which is not observed elsewhere.  
233



234

235 Figure 4: Predicted annual log-transformed abundance patterns of host-seeking *Ixodes ricinus* nymphs  
236 for the different sampling sites. The dots represent the maximum of each curve, i.e. the peak of  
237 abundance.

238

239 *Links between predicted tick abundance and temperature*

240

241 The predicted spring peak date can be related to the cumulative sum of temperatures from the  
242 beginning of the year, hence resulting in a degree-day effect (Figure 5). The order by which sites are  
243 ranked with respect to the cumulative temperature corresponds to the order of spring peak dates. The  
244 simulation exhibits an early peak in Gardouch and Carquefou, followed by Etiolles, La Tour-de-  
245 Salvagny, Velaine-en-Haye and Saint-Genès-Champanelle. For the four sites with the earliest spring  
246 peak, the peak occurs when temperature cumulative sum reaches *c.a.* 1000 °C.d (Table I). At the more  
247 continental site of Velaine-en-Haye, the maximum is reached at a lower value for the cumulative  
248 temperature. The mountainous site, Saint-Genès-Champanelle, appears to have a different behaviour  
249 regarding temperature, with a cumulative temperature around 1600 °C.d at peak date.

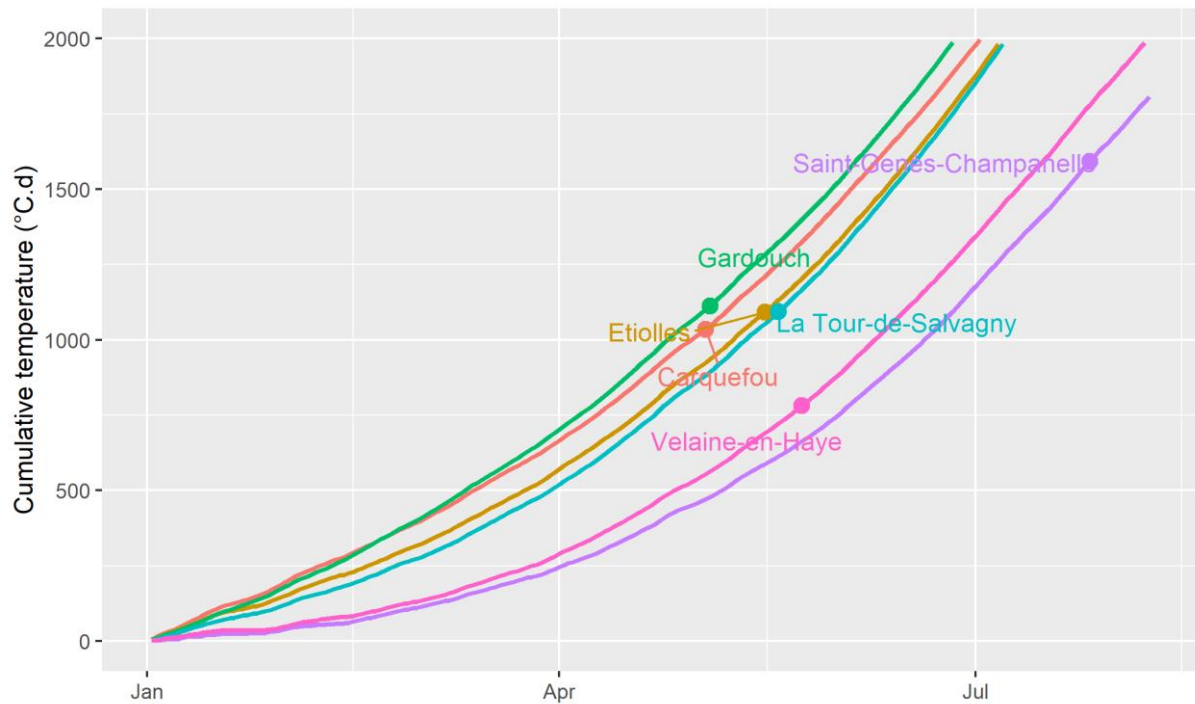
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256  
257  
258

Figure 5: Cumulative temperatures over time for the six locations, with dots corresponding on the X-axis to the predicted dates of *I. ricinus* host-seeking nymphal peak abundance at each location.

	Carquefou	Gardouch	Velaine-en-Haye	La Tour-de-Salvagny	Etiolles	Saint-Genès-Champanelle
Peak date (d)	May 2 (122)	May 3 (123)	May 23 (143)	May 18 (138)	May 15 (135)	July 25 (206)
Cumulative temperature (°C.d) at peak date	1034.5	1112.8	781.5	1093.3	1092.1	1593.2
Mean daily temperature (°C) at peak date	11.5	12.6	12.7	14.1	12.5	17.2

259 Table I: Peak date (predicted date of *I. ricinus* host-seeking nymphal peak abundance), cumulative  
260 temperature (°C.d) and mean daily temperature (°C) at peak date for the different locations.

261  
262 Table I shows the range of values of the mean daily temperature at the time of the peak between the  
263 different sites. The mountainous site of Saint-Genès-Champanelle shows again a clear different  
264 behaviour regarding temperature, with a peak of tick abundance corresponding to summer

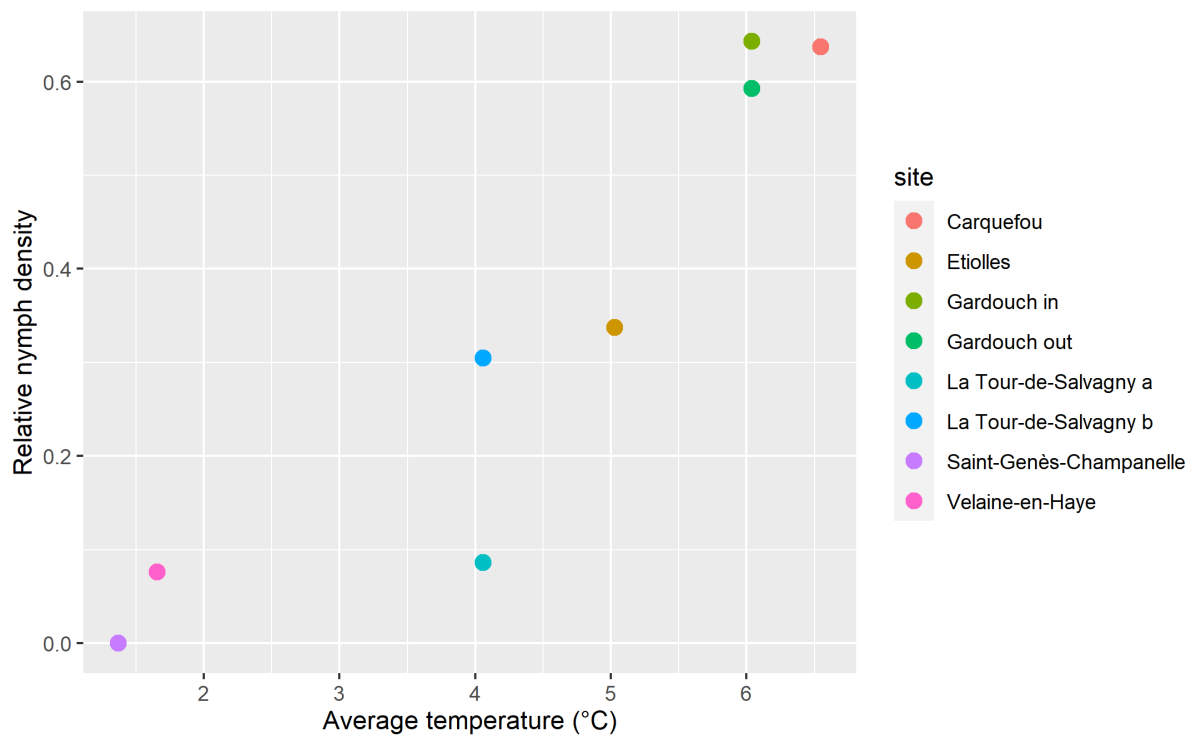
265 temperature (17.2°C). For the other sites, the peak of abundance is obtained in spring for intermediate  
266 temperature values, *i.e.* between 11.5°C (in Carquefou) and 14.1°C (in La Tour-de-Salvagny).

267

268 Moreover, average predicted tick abundance in January, standardized by the yearly maximum value at  
269 the corresponding site, can be directly related to the average temperature for the same period (figure  
270 6). This straightforward relationship shows that mild winter temperatures of Carquefou and Gardouch  
271 correspond to higher winter tick abundance than other sites.

272

273



274

275 Figure 6: Predicted mean nymph abundance in January, standardized by the yearly maximum value, as  
276 a function of corresponding mean temperature in January for the different sites.

277

## 278 Discussion

279

280 The tick abundance patterns modeled in this work can be divided into three types: two types exhibiting  
281 a unimodal curve, with a peak either in spring (Etiolles, La Tour-de-Salvagny, Velaine-en-Haye) or in  
282 summer (mountainous site of Saint-Genès-Champanelle), and a third type exhibiting a bimodal pattern  
283 in Carquefou and Gardouch, with a peak in spring, a minimum in summer and an increase with a  
284 plateau in autumn and winter. When comparing sites that exhibit a spring peak, the predicted peak  
285 occurs later as the site is located further east. Collected tick abundance declines thereafter in summer

286 in these sites, which might be due to a decrease in the host-seeking nymph population (due to the  
287 fixation of nymphs on hosts in the spring) or a decrease in the questing behaviour of the remaining  
288 nymphs due to a lower relative humidity in summer. These fitted tick abundance patterns are  
289 consistent with the literature. From Bregnard et al. (2021a) tick phenology is expected to be unimodal  
290 at northern latitudes and bimodal in areas with warmer and longer summers. They also reported 12  
291 different studies on tick phenology across Europe where the authors identified a unimodal or a bimodal  
292 phenology, but observed phenology does not always follow these rules, possibly due to year-to-year  
293 variations. Babenko (1958) (in Korenberg, 2000) depicts four stylized types of seasonal changes in the  
294 abundance of *I. ricinus* adults. More specifically, he considered bimodal curves for temperate zones  
295 (*i.e.* Crimea) and unimodal ones with a peak in summer for continental areas of Russia. Even applied  
296 to adult ticks, these curves can be compared to our predictions for the nymphal stage in Carquefou  
297 and Gardouch (oceanic and southwestern basin climate respectively), and in Saint-Genès-Champanelle  
298 (mountain climate), respectively. Concerning mountain climate, Bregnard et al. (2021a) show a cline  
299 ranging from bimodal to unimodal curves when reaching higher altitude (altitude ranging from 620 to  
300 1073 m). According to Gray et al. (2016), *I. ricinus* abundance patterns for larvae, nymphs and adults  
301 follow a bimodal curve in Central and Western Europe, but these authors also point out that there are  
302 variations on this expert-based pattern. Our fitted model based on harmonic regression and using  
303 longitudinal data resulting from 8 years of monthly surveys allows us to relate these seasonal variations  
304 to observations. It also suggests that these two types of patterns are both present in different locations  
305 of the French territory.

306  
307 The abundance patterns can be directly related to what we know about the specific climate of the  
308 different sites. A gradient in spring peak date is exhibited from the western sites located in temperate  
309 areas to the more eastern ones, corresponding to a continental climate (see the climate typology in  
310 France from Joly et al., 2010 on figure 1). Mountainous areas can be assimilated to even more  
311 continental zones, with however a heat deficit during summer. An early spring peak corresponds to  
312 temperate sites where temperatures are warmer in winter and at the beginning of spring. Diuk-Wasser  
313 et al. (2006) also highlighted an earlier peak for *Ixodes scapularis* nymphs in southern vs northern sites  
314 in USA. Temperature has long been identified as the major factor acting on tick development  
315 (Randolph, 2004), each stage necessitating a certain amount of degree-days to develop to the next  
316 stage (Hoch et al., 2010). The spring peaks in the different sites logically occur successively in  
317 accordance with the cumulative temperature curves (figure 5). Four locations (Carquefou, Etiolles,  
318 Gardouch and La Tour-de-Salvagny) exhibit a spring peak for comparable degree-day values (around  
319 1000 °C.d). This is not the case in Saint-Genès-Champanelle (around 1600 °C.d) and to a lesser extent  
320 in Velaine-en-Haye (around 800 °C.d). For the mountainous location, in Saint-Genès-Champanelle, a

321 peak is hardly identified in summer and the tick density curve looks smoothed, which generates  
322 uncertainty in the estimation of the peak date: the amount of degree-days may be over-estimated.  
323 Temperature data measured at 1.5 meter from the ground may not represent the temperature  
324 experienced by the ticks at ground level. Furthermore, factors other than cumulative temperature may  
325 influence the date of the peak. The date of the peak may depend on the proportion of larvae which  
326 are developing into nymphs during the spring: if development from larvae to nymphs occurs before  
327 the spring, *i.e.* in the autumn of the previous year (as suggested by Randolph et al., 2002), resulting  
328 host-seeking nymphs may be active very early in the spring, at the onset of warming. It has also been  
329 shown that the host-seeking behaviour (questing) of different tick populations may respond differently  
330 to temperature, depending on the considered climate (Tomkins et al., 2014). Ticks that have achieved  
331 their development start questing with a rate that depends on relative humidity and temperature.  
332 According to Beugnet et al. (2009), this proportion of questing ticks is maximal for intermediate  
333 temperatures, *i.e.* between 10 and 20°C. A field study also reported maximum values of collected ticks  
334 for intermediate temperatures in Germany (Gethmann et al., 2020), *i.e.* 13-15°C of ground  
335 temperature, which is comparable to our mean daily air temperature at peak date (table I). Our values  
336 for temperature at the peak are consistent with these expert- and data-based questing rates. Finally,  
337 a clear relationship has been shown between winter (January) abundance in host-seeking nymphs and  
338 corresponding average temperature in the different sites. This is supported by findings of Furness and  
339 Furness (2018), who showed a winter increase in the infestation of birds by immature *I. ricinus* ticks  
340 with temperature. As stated by Gray et al. (2009), climate change is likely to increase the duration of  
341 the host-seeking period of ticks, thus highlighting the need of winter tick collections to monitor the  
342 risk of tick bite.

343  
344 Relative humidity data, measured at 1.5 meter from the ground, were also available in the initial data  
345 set (Wongnak et al., 2022). However, no relationship was found between abundance and relative  
346 humidity, especially in summer (results not shown). Tick host-seeking activity in summer may be highly  
347 fluctuating due to very variable conditions of hygrometry, especially at ground level. Such an effect is  
348 difficult to demonstrate with monthly tick collections. Some experiments should specifically deal with  
349 this process, such as the ones carried out by Vail and Smith (1998) with a weekly sampling.

350  
351 Concerning inter-annual variations in tick abundance, we note that years with relatively high observed  
352 abundance compared to simulated abundance are not the same for different sites. While these  
353 variations can be explained by inter-annual variations of local meteorological conditions, other factors  
354 may also be involved, including host densities. Nymphal abundance is known to be related to the  
355 rodent abundance of the previous year, as shown by Perez et al. (2016) for the effect of wood mice

356 (*Apodemus sylvaticus*) abundance on *I. ricinus* densities. The indirect effect of beech fructification two  
357 years before on nymphal density and acarological risk (density of infected nymphs) has also been  
358 demonstrated respectively by Brugger et al. (2018) and Bregnard et al. (2021b).

359

360 In this study, tick abundance at different sites in France showed repeatable within year patterns across  
361 an 8-year period. At a given site, inter-annual variation was usually low compared to seasonal variation.  
362 The identified associations between climate characteristics and seasonal patterns of tick abundance  
363 corroborate expert opinions. Peak abundance usually occurred for cumulative temperatures of around  
364 1 000°C, with extremes of 780°C and 1600°C. The different profiles identified at the scale of France are  
365 a first step towards the understanding of tick phenology and its variation according to climate, and  
366 give new insight into the influence of climate change on tick activity that has to be put in perspective  
367 with disease risks.

368

#### 369 **Data availability**

370 The datasets generated during and/or analysed during the current study are available in the “TEMPO—  
371 Réseau National d’Observatoires de la Phénologie” repository, [https:// doi. org/ 10. 15454/ ZSYGUM](https://doi.org/10.15454/ZSYGUM).



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541  
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