

## 1 Systematic review and meta-analysis of *Hyalomma* 2 *marginatum* vertebrate hosts in the EU

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### 12

#### 13 Abstract

14 Host choice is a determining component of tick population and pathogen transmission  
15 dynamics. In Europe, ticks of the genus *Hyalomma*, which are involved in the transmission of  
16 several pathogens such as the Crimean Congo Haemorrhagic fever (CCHF) virus, are  
17 suspected to be spreading into new territories where they were previously unreported.  
18 Therefore, we performed a systematic review of the tick-host relationship of *Hyalomma* spp  
19 in Europe with a focus on *Hyalomma marginatum*, combined with a meta-analysis and meta-  
20 regression to describe its host preference pattern using three outcome values. Our initial  
21 qualitative analysis highlighted an increase in tick-host interaction rate in the last decades  
22 mostly in South-eastern and Central Europe. *H. marginatum* also appeared as the species  
23 holding the highest citation rate in terms of its association with hosts, and for which the  
24 largest number of host species were reported. The meta-analysis on *Hyalomma marginatum*  
25 host choice revealed preferential interactions for horses in the adult stage and birds of the  
26 *Emberizidae* and *Strigidae* families, in immature stages. Nevertheless, most of the  
27 heterogeneity of tick-host interactions remained unexplained suggesting the involvement of  
28 multiple drivers such as environmental or climatic conditions. Our results suggest that *H.*  
29 *marginatum* is a generalist tick whose distribution depends primarily on environmental  
30 conditions such as climate and habitat. Current limitations of our meta-analysis approach to  
31 identify hosts preference for *H. marginatum* and suggestions ways for improvement are  
32 further discussed.

33

## Introduction

34 Ticks are after mosquitoes, the second most important family of arthropod vectors involved  
35 in the transmission of vector-borne disease to humans. In Europe, the incidence of zoonotic  
36 tick-borne diseases such as anaplasmosis, Lyme borreliosis, Crimean-Congo Haemorrhagic  
37 Fever (CCHF) and rickettsiosis is increasing partly due to climate change (Gray et al., 2009).

38 Ticks (*Ixodidae*) are ectoparasites that require several hematophagous meals to complete  
39 their life cycle; thus, they alternate free-living and parasitic stages during their development.  
40 The non-parasitic stages include eggs, molting stages after blood-feeding, active or passive  
41 host searching stages after molting, and ovipositing females, are the most sensitive stages to  
42 environmental conditions. The transition from one development stage to the next one, except  
43 the emergence of larvae from eggs, requires blood feeding and therefore, the completion of a  
44 parasitic stage on a vertebrate host.

45 The range of host species on which a tick can feed varies depending on the development  
46 stages (e.g. usually immatures versus adults) and tick species. Most ticks require to feed on  
47 three-distinct hosts (to complete their development cycle (i.e. larvae, nymphs and adults  
48 feeding on different animals), but in some species the development cycle is completed on two  
49 (i.e ditropic) or even on a single (i.e monotropic) animal host. Some ticks are specialist while  
50 others are much more generalist. Historically, anatomical descriptions of tick mouthparts  
51 and coxae suggested that ticks had adapted to restricted groups of host species which they  
52 had co-evolved with, leading to the hypothesis that ticks were specialized parasites  
53 (Hoogstraal and Aeschlimann 1982). However, it was subsequently argued that constraints  
54 generated by environmental conditions during free-living stages were more critical to tick  
55 population fitness than those generated by host suitability and availability during parasitic  
56 stages, mainly because of the availability of a broad range of vertebrate host species to feed  
57 on (Klopmen et al. 1996). This statement was later supported by studies showing that host  
58 community abundance and specific composition had a limited influence in the geographical  
59 distribution of tick species (Cumming 2002; Nava and Guglielmone 2013; Estrada-Peña et  
60 al. 2020). The most straightforward approach to assess whether a tick species is a specialist  
61 is to consider the number of host species it can feed on (Lymbery 1989). However, other  
62 criteria such as the prevalence of infested hosts, the intensity of infestation or the  
63 phylogenetic distance between parasite hosts have also been considered relevant (Poulin  
64 and Mouillot 2003; Rohde 1980).

65 The specificity or genericity in the host choice is important as it has a direct impact on  
66 pathogen transmission and the possibilities of disease spillover. Indeed, a generalist tick that  
67 could feed on a large diversity of hosts and whose geographic distribution is barely limited  
68 by host availability, can contribute to the emergence of diseases through geographic  
69 expansion or interspecific pathogen transmission (McCoy, Léger, and Dietrich 2013; Dietrich  
70 et al. 2014). In addition, the density of generalist ticks is likely to increase as the number of  
71 species in the host community and/or the overall abundance of hosts increases. Because  
72 specialist ticks rely on a restricted number of host species and have a more limited potential  
73 in terms of geographic expansion, they are less likely to be involved in emergence events  
74 resulting from interspecific pathogen transmission or from tick colonization of new areas  
75 (McCoy, Léger, and Dietrich 2013; Dietrich et al. 2014). However, because of their high level

76 of adaptation to specific host species, populations of specialist ticks can locally thrive and  
77 contribute to the spread of their specific pathogens for which they are highly competent  
78 (Richard S. Ostfeld and Keesing 2000a).

79 In epidemiological systems involving a generalist vector, a vector-borne pathogen and  
80 multiple host species, the pathogen amplification transmission and maintenance potential  
81 may vary among the species of the available host community. In such systems, high species  
82 diversity can create a dilution effect resulting from the transmission of the pathogen to a wide  
83 range of hosts with low amplification, transmission and maintenance potential (Richard S.  
84 Ostfeld and Keesing 2000b; Schmidt and Ostfeld 2001). However, even if some hosts are  
85 poorly competent for the pathogen, they can still be good amplifiers of the tick and therefore  
86 contribute to boosting the tick population and thus, the potential number of infectious  
87 individuals. Therefore, there are less chances to observe a dilution effect in systems where the  
88 tick vector is a specialist species (Occhibove et al., 2022).

89 Tick species belonging to the *Hyalomma* genus are involved in the transmission of several  
90 important pathogens such as the Crimean Congo Haemorrhagic Fever (CCHF) virus.  
91 Immature *Hyalomma* specimens feed mainly on birds and small mammal species belonging  
92 to the order *Rodentia* and *Lagomorpha* while the adults feed mostly on species belonging to  
93 the *Bovidae* family (Spengler and Estrada-Peña, 2018). However, the range and number of  
94 hosts involved in the *Hyalomma* spp. life cycle varies greatly across species. For example, *H.  
95 aegyptium* is a three-hosts tick that feeds mainly on *Testudo* tortoises (Široký et al., 2006).  
96 However, human and others vertebrates can act as occasional hosts. *H. dromedarii* is a two-  
97 hosts tick (occasionally one or three) mainly found on camels. *H. scupense* is a one or two  
98 hosts species that feeds preferentially on domestic ungulates, especially horses (*Equus ferus  
99 caballus*), and cattle (*Bos taurus*), regardless of its stage (Apanaskevich, 2004; Apanaskevich  
100 et al., 2013). Conversely, *H. rufipes* and *H. marginatum* tend to be more generalist (Estrada-  
101 Peña et al., 2018). Tick species belonging to the *Hyalomma* genus are involved in the  
102 transmission of several important pathogens of bacterial (rickettsial, anaplasma species),  
103 parasitic (theileria species) and viral origin such as the Crimean Congo Haemorrhagic Fever  
104 (CCHF) virus (Bakheit et al., 2012; Kumar et al., 2020). *Hyalomma marginatum* is one of the  
105 main vectors of the virus which is, currently considered as an emerging disease in Europe,  
106 Africa, Asia and the Middle East.

107 *H. marginatum* is a ditropic tick. This implies that larvae and nymphs feed on the same host,  
108 which is usually a small vertebrate (a lagomorph, a bird, a hedgehog or a rodent), whereas  
109 the adults usually feed on large ungulates such as horses, cattle, sheep, goats, wild boars,  
110 cervids or occasionally humans (Apanaskevich 2004). Considering its wide host range and  
111 its wide geographical distribution, *H. marginatum* could be considered as a generalist tick.  
112 However, host preferences have been reported at least for the adult stage (Grech-Angelini  
113 et al. 2016).

114 Furthermore, considering the hypothesis of “global generalist and local specialist” recently  
115 developed by McCoy, Léger, and Dietrich (2013), ticks would locally develop preferences  
116 and adaptations to the most largely available host species leading to variations in the host  
117 species preference patterns across their distribution range. Under this hypothesis, an  
118 assessment of host preference at a wide scale would lead to falsely consider a tick species

119 as generalist. Conversely, observation at the scale of the tick species distribution range of  
120 higher tick densities on certain host species, could result from the confounding effect of  
121 climate and habitat conditions rather than from genuine tick host preferences, and could  
122 thus lead to false conclusions regarding its classification as a generalist or specialist vector.

123 In this study, we conducted a systematic review of tick-host interactions of the *Hyalomma*  
124 species present in Europe in order to characterize the host community interacting with  
125 *Hyalomma* genus in Europe. Subsequently, we implemented a meta-analysis specifically on  
126 *H. marginatum* in order to describe its host species range, assess its host preference pattern  
127 and discuss its classification as a generalist or as a specialist tick species. Finally, based on  
128 those results, we discussed the potential influence on the most often reported host species  
129 on the tick life cycle and on the circulation of its vector borne pathogens such as CCHF.

130 **Materials and methods**

131 We followed a systematic review approach, with the goal to extract any information related  
132 to *Hyalomma* spp tick-host interactions in Europe available in the literature from 1970 to  
133 2021. The systematic review was conducted following as closely as possible PRISMA  
134 (Preferred Reporting Items for Systematic Reviews and meta-analysis) guidelines (Page et  
135 al., 2021).

136 **Publication selection**

137 To achieve that goal, literature searches were carried out in the following databases:  
138 BIOSIS, CAB, Embase, MEDLINE, PubMed, Scopus and Web of Science. Publications were  
139 selected through specific keywords for Title (K1), abstract (K2) and within the core text  
140 (K3). The first list of keywords consisted of an enumeration of all *Hyalomma* species that  
141 can be found in Europe (Estrada-Peña et al., 2018) which were combined into query K1.  
142 The second list of keywords consisted of a list of species common names, families or clades  
143 that could act as potential hosts of *Hyalomma* ticks and were integrated into query K2. The  
144 third list of keywords consisted of an enumeration of all the countries within Europe which  
145 formed query K3 (Table 1).

146 **Table 1:** Queries used for the title (K1), abstract (K2) and body (K3) in the systematic  
147 literature review.

K1	K2	K3
( <i>Hyalomma</i> OR <i>marginatum</i> OR <i>aegyptium</i> OR <i>anatolicum</i> OR <i>rufipes</i> OR	animals OR ruminants OR ungulates OR vertebrates OR Cervidae OR birds OR livestock OR cattle OR hares OR rabbits OR	Albania OR Andorra OR Armenia OR Austria OR Azerbaijan OR Belarus OR Belgium OR 'Bosnia and Herzegovina' OR Bulgaria OR Croatia OR Cyprus OR Czechia OR Denmark OR Estonia OR Finland OR France OR Georgia OR Germany OR Greece OR Hungary OR Iceland OR Ireland OR Italy OR Latvia OR Lithuania OR Luxembourg OR Malta OR Monaco OR Montenegro OR Netherlands OR

K1	K2	K3
scupense OR plumbeum OR lusitanicum ) AND (tick OR host)	reptiles OR hedgehogs OR lagomorphs OR deer OR horses OR sheep OR goat OR Turdidae OR boar	'North Macedonia' OR Norway OR Poland OR Portugal OR 'Republic of Moldova' OR Romania OR 'Russian Federation' OR Russia OR 'San Marino' OR Serbia OR Slovakia OR Slovenia OR Spain OR Sweden OR Switzerland OR Turkey OR Ukraine OR 'United Kingdom' OR Wales OR Scotland OR 'Northern Ireland' OR England

148 In addition to the keywords, inclusion and exclusion criteria were defined. Indeed, only  
149 original data collected in natural habitats on the trophic relationships of ticks of the genus  
150 *Hyalomma*, (i.e. a tick detected on a host), were included. As such, strict modeling studies,  
151 reviews and laboratory experiments were excluded. Moreover, we reduced our screening to  
152 publications which were in English or French. No exclusion criteria were applied related to  
153 the time of publication as it is supposed that host preferences should be constant across  
154 time, but we restricted the geographical area of the study to Europe. The choice of  
155 European countries was based on the list set up by the World Health Organisation's  
156 Regional Office for Europe, which includes Europe in the broadest sense. In order to get a  
157 more homogenous geographical and environmental context, Central Asian countries  
158 (Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan) was considered too  
159 different from those in Europe considered, and therefore removed from the targeted list of  
160 countries chosen for the study. Finally, publications whose access was restricted  
161 (publications that were too old and present only in the archives, or whose full texts were  
162 not accessible) could not be included in our study.

163 Duplicates between databases were removed in Zotero (Roy Rosenzweig Center for History  
164 and New Media, 2022) and selected publications were imported into Rayyan, which is an  
165 open access software (Ouzzani et al., 2016) designed for the collaborative implementation  
166 of systematic reviews, scoping reviews and other knowledge synthesis projects, by  
167 speeding up the process of selecting studies through easy screening of titles and abstracts.

## 168 **Data extraction and compilation**

169 After careful evaluation of the inclusion criteria in Rayyan, a full-text review was conducted  
170 on selected articles to extract pertinent data. A first database was compiled including the  
171 following qualitative data: title, authors, date of publication, country region or sub-region of  
172 the study and if available, date of sampling, host species and *Hyalomma* tick species  
173 involved, life stages of the sampled ticks as well as a classification of the invasive status of  
174 the collected ticks (imported or resident). The compilation of this shortlist allowed us to  
175 extract the following additional quantitative variables for each sampled host species:  
176 number of examined hosts, number of hosts infested by *H. marginatum*, number of *H.*  
177 *marginatum* ticks collected, and number of ticks collected in total. This data-extraction step  
178 was verified and validated by two different team members to reduce potential study  
179 miscount and misclassification errors.

180 In addition, to complete the geographical information related to each study, we extracted a  
181 measure of the most dominant landscape in which the sampling was conducted as well as  
182 the suitability of this habitat for the occurrence of *H. marginatum*. In order to do so, we  
183 relied on two raster maps, respectively: LANMAP 3 and the *H. marginatum* Suitability Map  
184 in Europe from Estrada-Peña and Wint (2016). LANMAP is a European landscape  
185 classification with four hierarchical levels, using digital data on climate, altitude, geological  
186 material and land cover as determinant factors (Mücher et al., 2010). It provides 350  
187 landscape types, at the most detailed level, with 14000 mapping units with a minimum  
188 mapping unit of 11 km<sup>2</sup>. For the meta-analysis, we used a level of detail sufficient for  
189 distinction between climates.

190 The *H. marginatum* Suitability Map in Europe (Estrada-Peña and Wint 2016), used MODIS  
191 satellite data of daytime land surface temperature and the Normalized difference vegetation  
192 index at a 1km spatial resolution as predictive covariates for tick's occurrence in a  
193 statistical regression model. Values from these two raster maps were extracted at the  
194 lowest geographical scale reported in each publication. Specifically, we computed the mean  
195 value of the suitability of *H. marginatum* within the region/subregion or country sampled  
196 and we extracted the most dominant landscape within the sampling zone being the  
197 region/subregion or the country.

## 198 Data analysis

199 A Meta-analysis was then carried out on data extracted specifically for *H. marginatum*. The  
200 quantitative outcome, also called effect size, from various separate studies was pooled  
201 together in a statistical model to provide an estimate of the combined effect size and error.  
202 The effect sizes from several studies were expressed on the same scale, and each effect size  
203 corresponded to a particular outcome. Moreover, effect sizes were weighted in such a way  
204 that precise estimates (those with lower sampling error) had a higher influence on the  
205 pooled effect size than inaccurate ones. We investigated three effect sizes: 1. Proportion of  
206 hosts infested by *H. marginatum* among hosts examined for ticks, as a proxy of infestation  
207 rate; 2. Proportion of *H. marginatum* ticks among the total number of ticks collected on the  
208 hosts, as a proxy for competitiveness of the tick species; 3. Mean number of *H. marginatum*  
209 ticks collected per host, as a proxy of the parasitic load.

210 We used a random-effects model to partially pool the effect size, given the diversity of  
211 contexts involved in the original studies. Indeed, even after accounting for sampling error,  
212 an additional source of variation between studies was expected (Senior et al., 2016). This  
213 variation is referred as heterogeneity. Some studies in our meta-analysis contributed more  
214 than one observed effect size as they could report interactions of *H. marginatum* with more  
215 than one host species. Thus, heterogeneity was measured among records of interactions of  
216 *H. marginatum* with a host species in a study (publication) rather than among studies per  
217 se. The heterogeneity variance  $\tau^2$  was calculated using the restricted maximum likelihood  
218 estimator for continuous effect sizes and the maximum likelihood estimator for proportions  
219 (Viechtbauer 2005). Among the various measures of heterogeneity that can be quantified  
220 based on  $\tau^2$ , we used the  $I^2$  statistic.  $I^2$  can be conceptualized as the proportion of variation  
221 in effect sizes that cannot be assigned to sampling error (Higgins and Thompson 2002).  
222 Thanks to its benchmarks it makes comparison of heterogeneity between meta-analyses

223 easy. These benchmarks define small, medium, and high  $I^2$  as 25%, 50%, and 75%,  
224 respectively (Higgins et al. 2003).

225 Hosts, climate and environmental suitability were used as factors to explain the  
226 heterogeneity among effect size values retrieved from the selected studies. Thus, subgroup  
227 meta-analysis and meta-regression were conducted. In order to have a meaningful numbers  
228 of observations per category, hosts were grouped by family rather than species  
229 (e.g. *Caprinae* for sheep and goat, *Cervidae* to include red deer (*Cervus elaphus*), roe deer  
230 (*Capreolus capreolus*) and fallow deer (*Dama dama*), and bird families instead of bird  
231 species. Subgroups meta-analysis for the categorical variables (hosts and climate), and  
232 meta-regressions for the continuous variable (Suitability) were conducted. In a subgroup  
233 meta-analysis, it is hypothesized that effect sizes from different studies do not stem from  
234 the same general population but are rather divided in subgroups, each of which has a  
235 unique distinct overall effect. These subgroup effects are estimated, and a null-hypothesis  
236 significance test is performed assuming the absence of differences between subgroups.  
237 Cochran's Q statistic (Cochran 1954) was employed to measure the differences between the  
238 estimated effect sizes and compared to its theoretical  $\chi^2$  sampling distribution under the  
239 null hypothesis. Since effect-size estimates of subgroups based on fewer than 5 studies  
240 could lead to inaccurate estimations of  $\tau^2$  (Borenstein et al., 2021). we assumed that  
241 subgroups shared a common estimate of the among-studies heterogeneity, in order to  
242 minimize this bias in  $\tau^2$  estimation.

243 In a meta-regression, the outcome (response variable) is predicted according to the values  
244 of quantitative explanatory variables, similar to multiple regression. The outcome is the  
245 effect size, and the explanatory variables are quantitative characteristics documented in the  
246 different studies that can have an impact on effect size. We conducted this analysis on adult  
247 and immature stages separately, as their hosts belonged to different zoological families.

248 As a significant proportion of the interaction records concerned birds, we investigated if  
249 their behavior (feeding, migration) could explain the observed differences in the three  
250 outcomes used in the meta-analysis, respectively infestation rate, competitiveness and  
251 parasitic load. Bird behavior was condensed in a single parameter according to the feeding  
252 behavior and the migratory status of each species, as such they were classified in three  
253 categories: - 1 Birds spending time on the ground and not migrating - 2 Birds spending time  
254 on the ground and migrating - 3 Birds not spending time on the ground and migrating.  
255

## 256 **Assessemment of the potential Impact of bird behaviour**

257 In order to correlate this behavior parameter to the three outcomes, we run three  
258 generalized linear model in the *brm* package after specifying informative priors for the  
259 model parameters. The prior distribution for behavior was modelled as a normal  
260 distribution (0,2), as we expected small estimate due to our limited number of studies.  
261 We employed a zero inflated beta regression to model the relationship between infestation  
262 rate and behavior. To meet model assumptions, we substracted each value of infestation  
263 rate from 1 as it was initially an excess of 1.  
264 Concerning the relationship between competitiveness and behavior, we employed a beta  
265 regression to model.

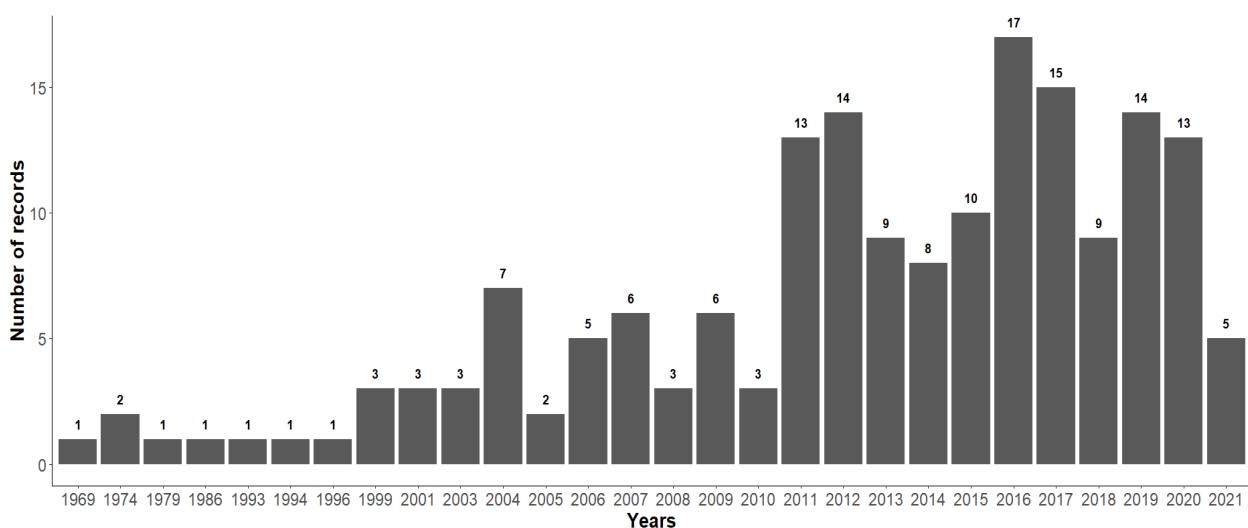
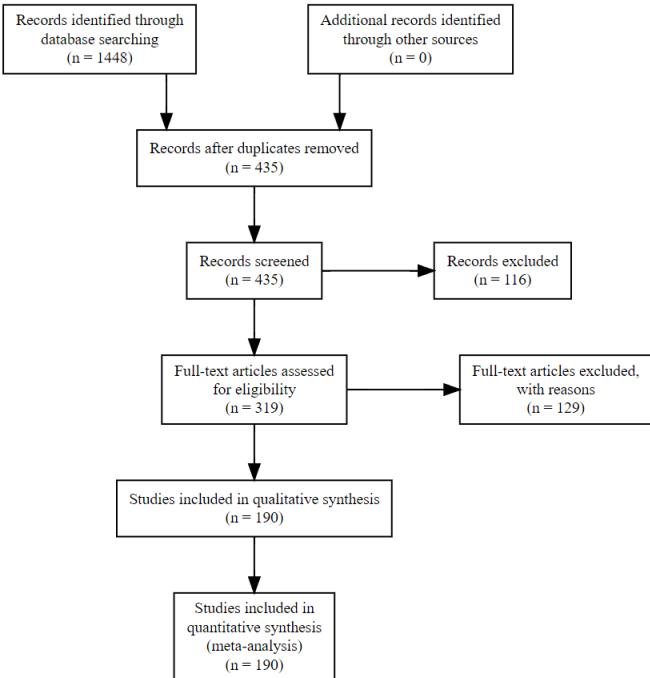
267 For the relationship between parasitic load and behavior we employed a quasi-poisson  
268 distribution for modeling.  
269 The Bayesian regression model was expressed as:  $Y \sim X1 + \varepsilon$ , where  $Y$  the response variable  
270 is one of the three outcomes and  $X1$  is the behavior as a predictor variable.  
271 We mostly used default *brm* settings, including four chains, which were run for 2000  
272 iterations and discarding the first 1000 as a burn-in period. We used default priors except  
273 for behavior estimate, for which we selected a narrower prior considering the numerous  
274 confounding factor among the studies from which the values were extracted. Specifically,  
275 we used normally distributed priors with a mean of one and a standard deviation of 2.  
276 For each metric, response we calculated the proportion of the posterior distribution of the  
277 mean comparative behavior estimate (corresponding to the intercept against one of the  
278 level of the factor) above or below zero, equivalent to the probability of an increasing or  
279 decreasing mean outcome comparatively to bird behavior.  
280 The average marginal effect of each factor level of bird behavior was also investigated.  
281 Furthermore, to visualize the posteriors for birds behavior we used a hypothetical dataset  
282 to generate predictions using 4000 draws.  
283 Statistical analyses were conducted using the R statistical software version 4.3.2 (R Core  
284 Team, 2023) with the packages *meta* (Schwarzer 2022), *metafor* (Viechtbauer 2022) and  
285 *brm* (Bürkner 2021).

286 **Results**

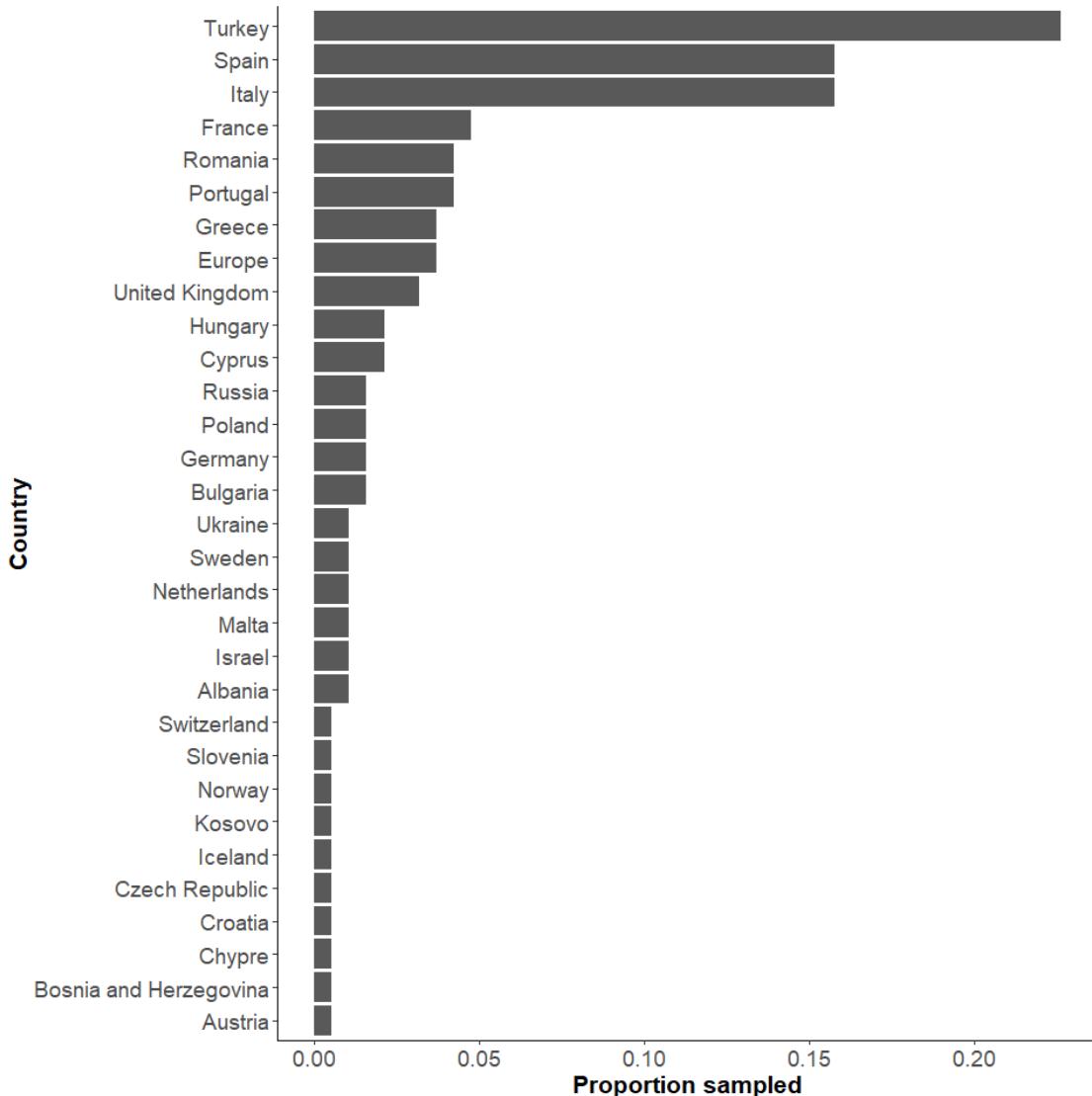
287 **Bibliometric outputs**

288 The initial query of the seven target data bases yielded 1448 records, which reduced to 435  
289 articles after removing duplicates. Among these, 319 references were selected for full  
290 reading during the first phase of selection by title and abstract, using Rayyan. A total of 100  
291 references could not be exploited, either because the full text was unavailable or because  
292 they were written in a language other than French or English. The remaining 219 articles  
293 were read, and three of them were finally discarded because they were considered  
294 irrelevant. The remaining 219 publications were included in the qualitative analysis, 190 of  
295 them providing sufficient details to be included in the quantitative analysis (Figure 1).

296



307 The selected publications covered 29 countries. Among them, Turkey was the most  
308 represented with 23% of the selected publications, followed by Italy and Spain representing  
309 16% of the selected publications each (Fig 3).



310

311 **Figure 3.** Proportion of publications selected for quantitative analysis by country

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313

### Qualitative analysis on the different *Hyalomma* tick species

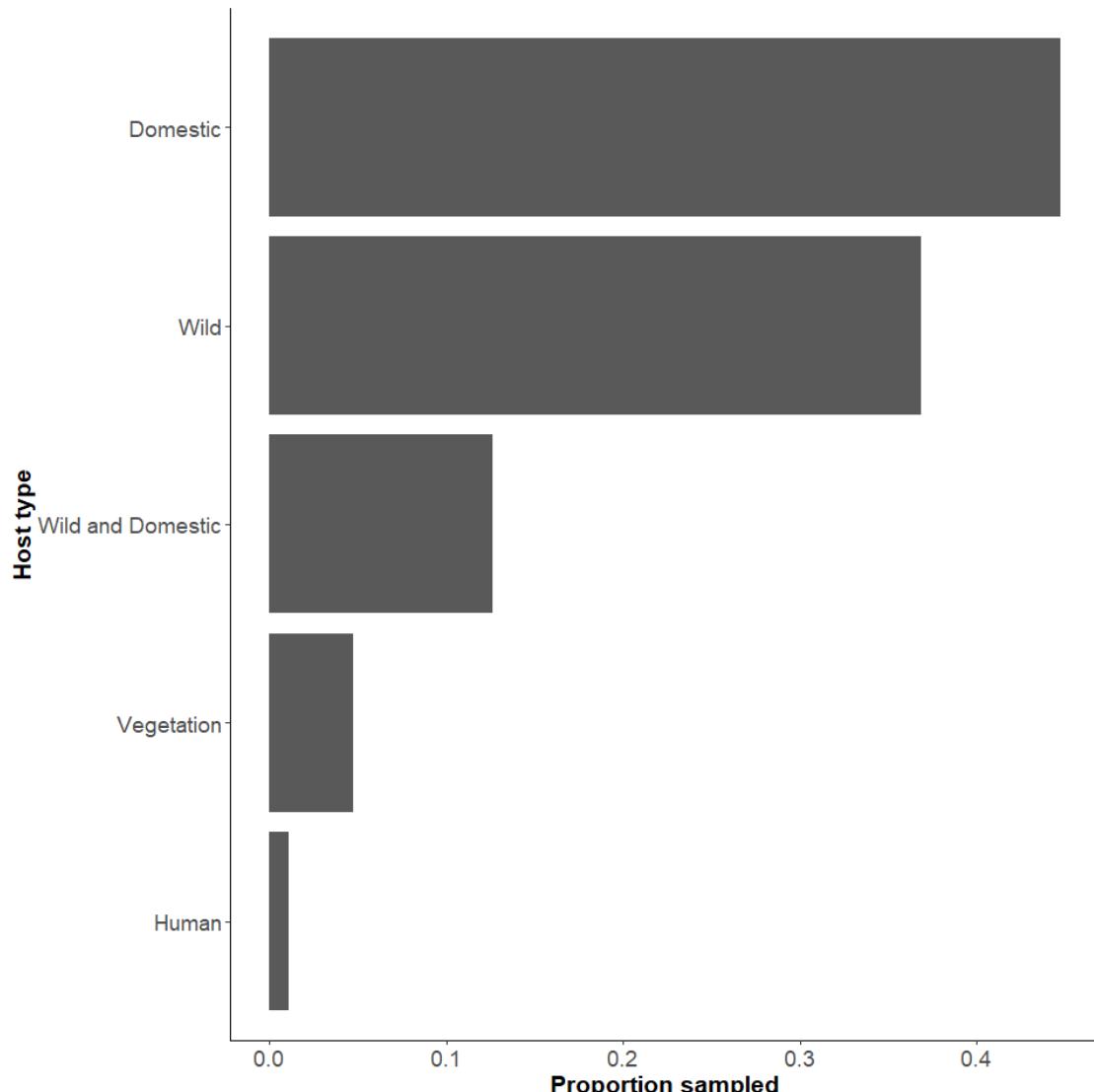
314

Among the 190 remaining publications, 85 papers (45%) reported only interactions with domestic hosts, 70 (37%) only with wild hosts and 24 (12%) with both (wild and domestic hosts). A total of 9 papers (5%) concerned ticks in free questing stages on vegetation and 2 (1%) were human case reports (Figure 4).

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**Figure 4.** Sampling effort for each host type

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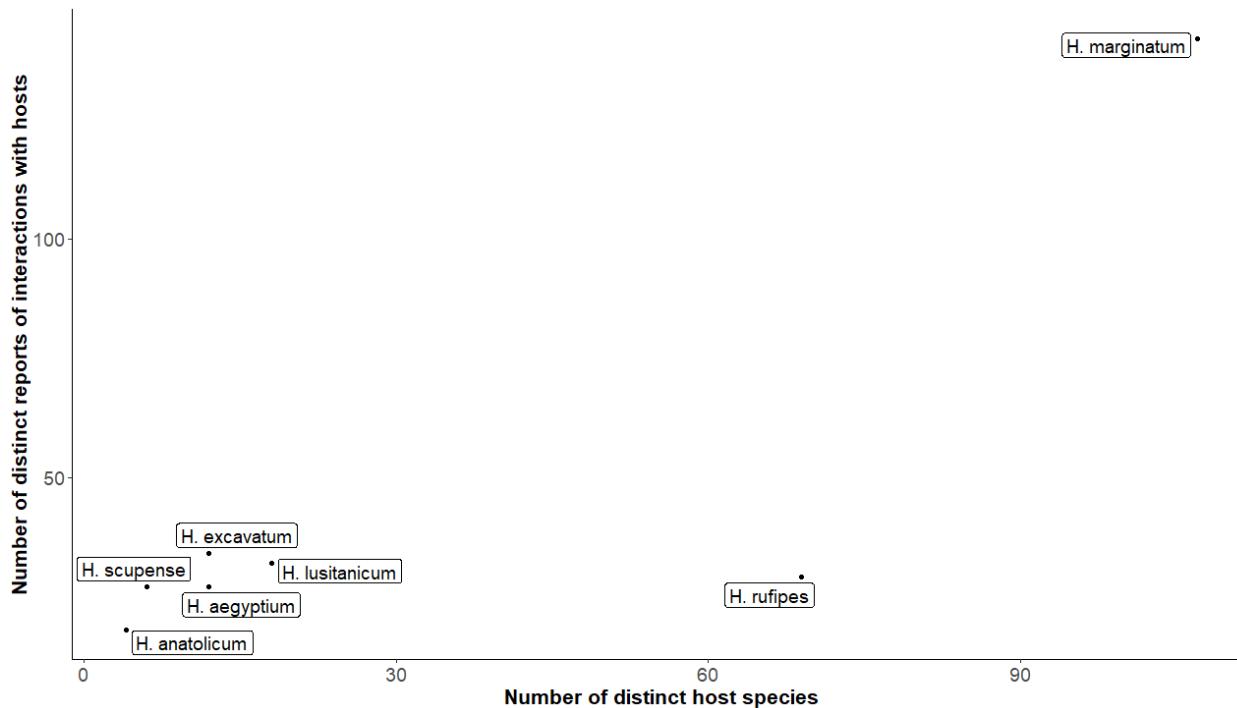
320

321      **Table 2:** Number of host species infestation distinct records for each *Hyalomma* species. Each citation  
322      represents one report of a tick species infesting one host species reported in a publication.

Species	Number of records	Percentage
<i>Hyalomma marginatum</i>	142	41
<i>Hyalomma excavatum</i>	34	10
<i>Hyalomma lusitanicum</i>	32	9
<i>Hyalomma rufipes</i>	29	8
<i>Hyalomma scupense</i>	27	8
<i>Hyalomma aegyptium</i>	27	8
<i>Hyalomma unspecified</i>	22	6
<i>Hyalomma anatomicum</i>	18	5
<i>Hyalomma dromedarii</i>	3	1
<i>Hyalomma asiaticum</i>	2	1
<i>Hyalomma impeltatum</i>	2	1
<i>Hyalomma truncatum</i>	2	1
<i>Hyalomma turanicum</i>	2	1

323      Twelve species belonging to the *Hyalomma* genus were reported in Europe. The most  
324      common was *H. marginatum* with 142 citations (42%) (Table 2).

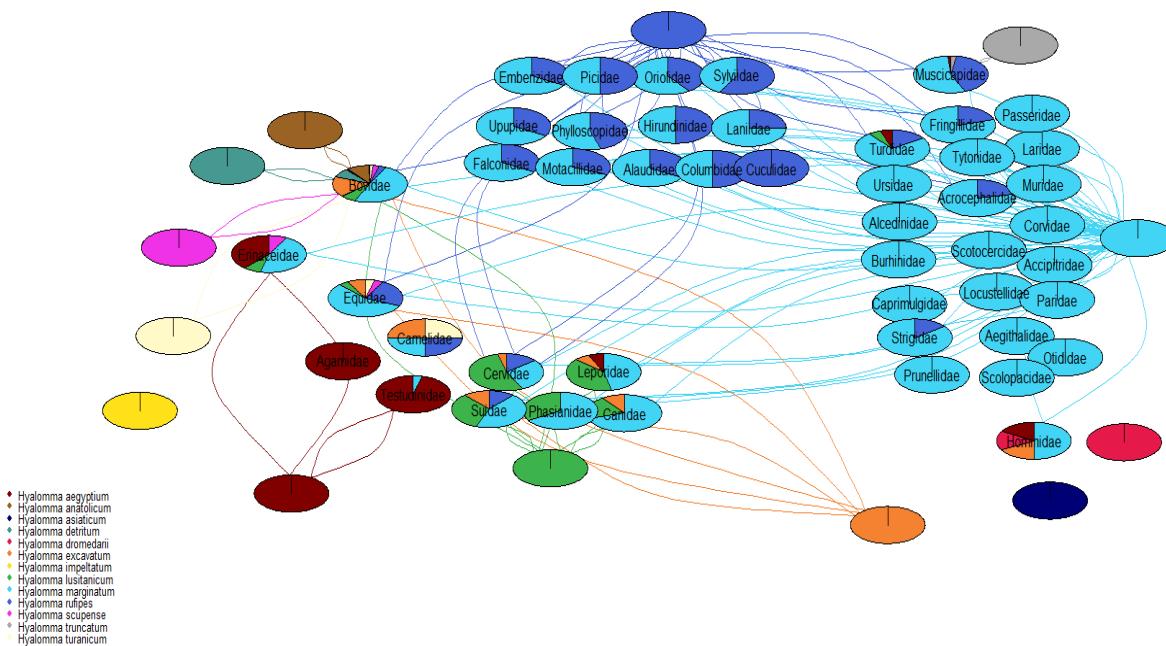
325      Among *Hyalomma* species, the number of distinct reports of interactions with hosts and the  
326      number of reported hosts species were positively correlated. As such, *H. marginatum* was  
327      the *Hyalomma* species with the highest number of reported host species in our study  
328      (Figure 5). The second was *H. rufipes* even though its number of distinct records of  
329      interactions with hosts was relatively low (n=27). For the remaining five commonly  
330      reported *Hyalomma* species, the number of hosts was below twenty, possibly due to their  
331      lower number of distinct records of interactions with hosts.



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**Figure 5.** Number of distinct tick-host interactions reports in relation to the number of hosts distinct host species reported in *Hyalomma* tick species.



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**Figure 6.** Network of tick-host interaction, in which each node pie represents a family of hosts, and the proportion of each node pie is relative to the number of recorded interactions of the \*Hyalomma\* species of the same color. Only interaction which were reported at least two time are connected by an edge. \*Hyalomma\* species are not labelled as the legend describes the color associated with each \*Hyalomma\* species.

340 Figure 6 illustrates the distribution of *H. marginatum* across various host families, with the  
341 exception of the Agamidae family, indicating a broad diversity primarily driven by the  
342 presence of immature stages, particularly among avian families. *H. rufipes*, the second most  
343 frequently reported tick species, shows a narrower host range, primarily including mammal  
344 (*Equidae, Cervidae, Leporidae, Suidae, Erinaceidae, Canidae, Bovidae*) and bird (*Phasianidae,*  
345 *Turdidae*) families. On the other hand, *H. lusitanicum* was predominantly associated with  
346 wild host families such as *Cervidae* and *Suidae*, with limited reports within families  
347 representing domestic animals like *Bovidae* and *Equidae*. Similarly, *H. excavatum* was more  
348 associated with for wild host families, albeit with occasional reports on *Equidae, Bovidae*,  
349 and human hosts.

350 Fewer host families were reported for *H. aegyptium*, *H. anatolicum*, and *H. scupense*, as  
351 expected from the low number of distinct reports of interactions with hosts for these  
352 *Hyalomma* species. *H. aegyptium* was prominently associated with reptiles, particularly the  
353 *Agamidae* and *Testudinidae* families, with additional reports in wild host families like  
354 *Leporidae* and *Testudinidae*, along with sporadic reports on human hosts. Meanwhile, *H.*  
355 *anatolicum* and *H. scupense* primarily infest domestic hosts within the *Bovidae* and *Equidae*  
356 families, with *H. anatolicum* exclusively reported in the *Bovidae* family.

### 357 **Quantitative analysis on *H. marginatum***

358 Table 3 presents a summary of the effect sizes for the three predefined outcomes  
359 (infestation rate, competitiveness, and parasitic load) of the meta-analysis, estimated from  
360 the 75 relevant publications presenting quantitative data on the interactions between  
361 vertebrate hosts and *H. marginatum*. The number of reported interaction records differed  
362 greatly by development stage and outcome. On average, there were many more records for  
363 immature stages than for adult stages. The infestation rate was less reported than the two  
364 other outcomes for both stages. The estimates of effect size were quite similar across  
365 developmental stages, except for mean competitiveness, which was considerably higher in  
366 immature stages than in adult stages. Regardless of the effect size, confidence intervals are  
367 large and the heterogeneity between tick host interaction records was substantial (Table 3),  
368 which suggests the existence of several factors including host preferences or sampling  
369 biases, which deserve further investigation.

370

371      **Table 3:** Summary of the effect-size estimates with their 95% confidence interval and the estimated  
372      heterogeneity ( $I^2$ ) for the three target outcomes by developmental stage. The infestation rate is measured by  
373      the proportion of hosts infested by *H. marginatum* among hosts examined for ticks; the competitiveness by the  
374      proportion of *H. marginatum* in relation to the total number of ticks collected on the hosts; and the parasitic  
375      load by the average number of *H. marginatum* collected per host. Results are broken down by stage, as *H.*  
376      *marginatum* is predicted to feed on very different hosts in immature and adult stages, as all ditropic ticks.

Development stage	Effect size	Number of interaction records	Estimated effect size	95% Confidence Interval	Among interaction records heterogeneity ( $I^2$ in %)
Adult	Infestation rate*	14	0.106	0.003;0.296	90.7
	competitiveness**	39	0.080	0.038;0.016	99.6
	Parasitic load***	36	1.625	0.59;2.661	99.8
Immature	Infestation rate*	45	0.091	0.057;0.141	80.5
	competitiveness**	78	0.781	0.583;0.901	84.2
	Parasitic load***	63	0.064	0.045;0.083	78.3

377      \* proportion of animals \*\* proportion of ticks \*\*\* mean number of ticks per animal

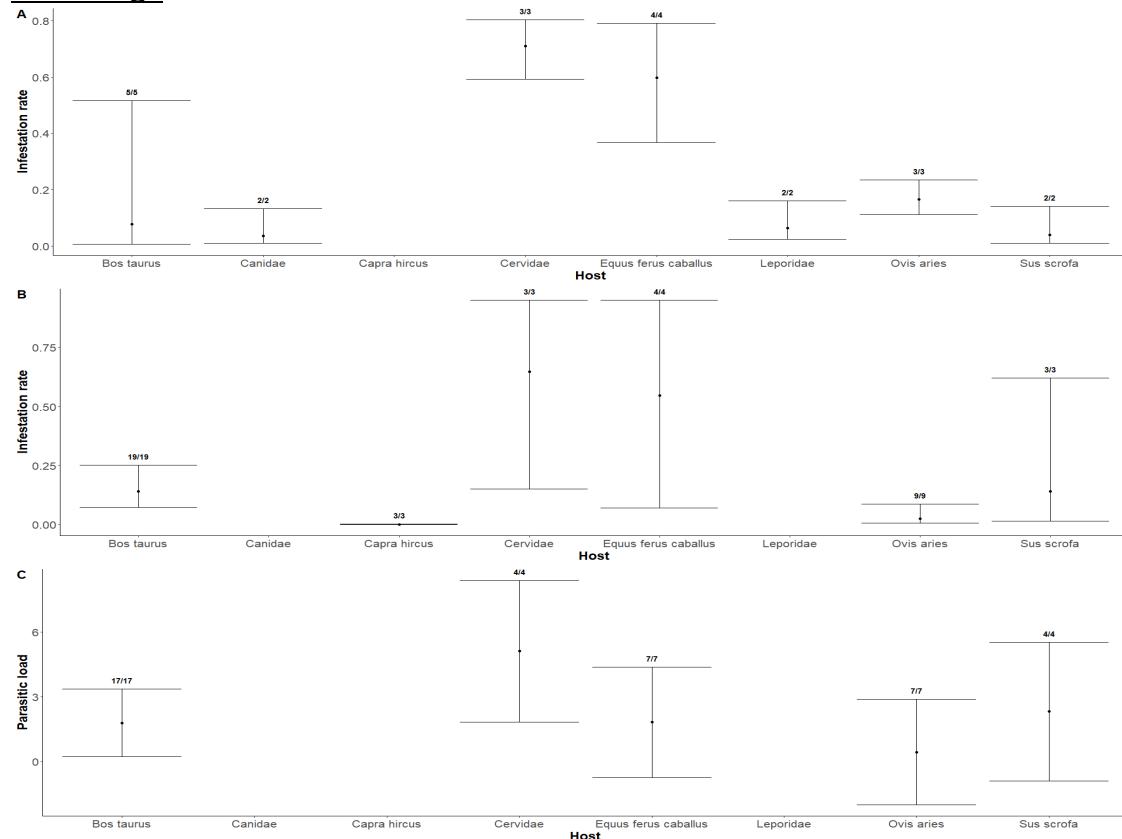
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## Host effect

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### Adult stage



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**Figure 7.** Effect of host taxonomic group on (A) infestation rate (B) competitiveness (C) parasitic load for adult stage. Effect size are represented with their 95% confidence intervals. The numbers on top of the error bar correspond to the number of distinct reports of interaction with host against the number of publications.

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We generally observed a relatively high imprecision (A max of 0.51 difference between the lower and upper estimates) in the estimated pooled effect sizes across tick-host interaction for each taxonomic regardless of the effect size (Figure 7). Infestation rate and competitiveness of *H. marginatum* differed significantly among host taxonomic groups (Respectively  $Q=98.44$ ,  $p\text{-value}=<0.0001$ ;  $Q = 138.30$ ,  $p\text{-value}=<0.0001$ ) (Supplementary S1; Supplementary S2). No significant difference was found among host taxonomic groups for parasitic load ( $Q= 5.15$ ,  $p\text{-value}=0.2722$ ).

393  
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Competitiveness of *H. marginatum* was lower in *Caprinae* (*Ovis aries*, *Capra hircus*), *Canidae*, *Leporidae* and wild boar (*Sus scrofa*) in comparison to others host taxonomic groups.

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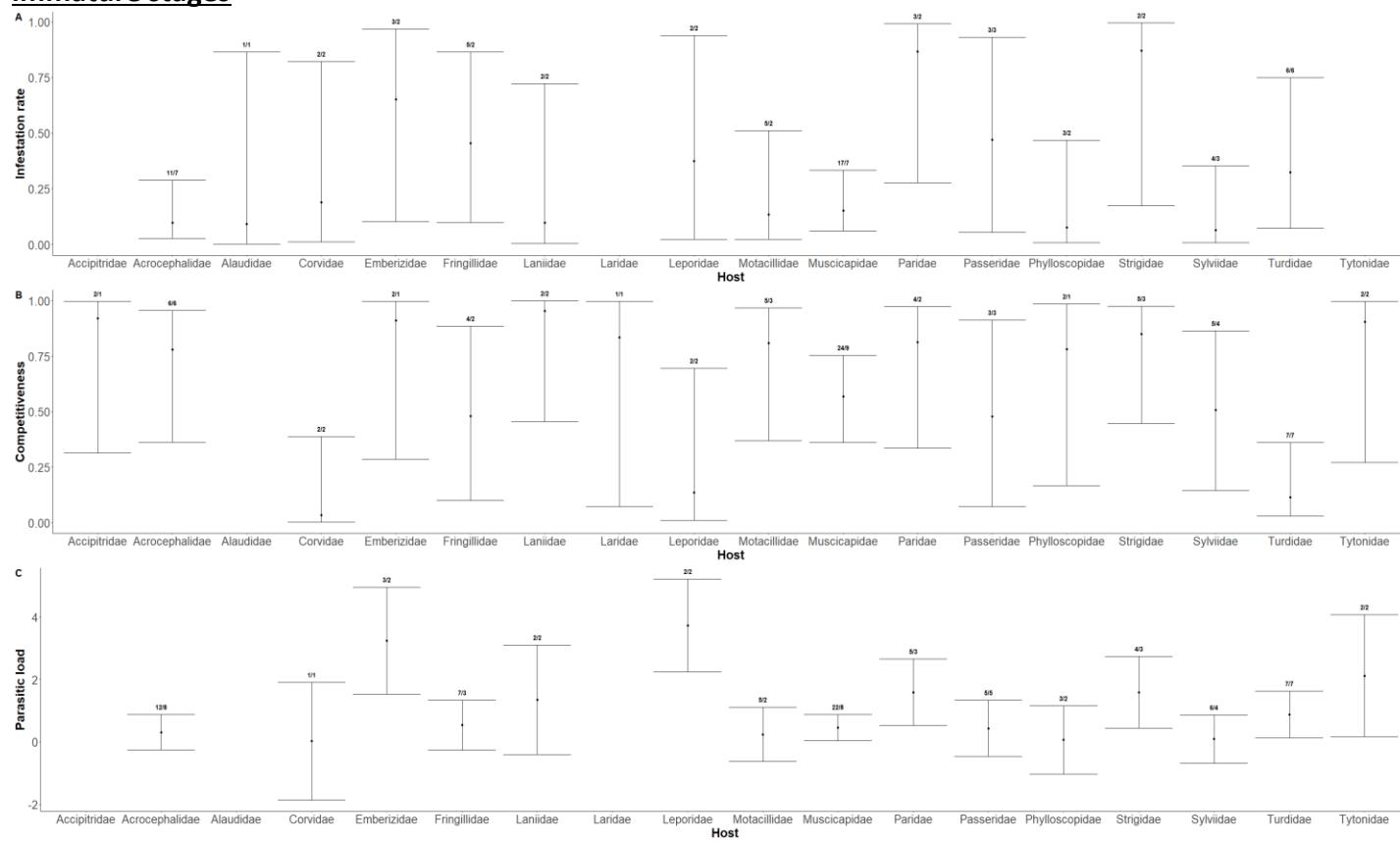
Pooled effect sizes were generally higher in Horses, and Cervidae than in the other host taxonomic groups.

397  
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Residual heterogeneity  $I^2$  after accounting for host effect was 88.3%, 99.6%, 99.7% for infestation rate, competitiveness and parasitic load, respectively.

399

### Immature stages



400

401 **Figure 8. Effect of host species on (A) infestation rate (B) competitiveness (C) parasitic load for immature stages.**  
402 Effect size are represented with their 95% confidence intervals. The numbers on top of the error bar correspond  
403 to the number of distinct reports of interaction with host against the number of publications

404 Similarly to the meta analysis for adult stages, we observed imprecise pooled effect size for  
405 most of the families of immature *H. marginatum* hosts regardless of the chosen effect size  
406 (Figure 8).

407 Significant differences were detected among host families for competitiveness and parasitic  
408 load (Respectively,  $Q=41.18$ ,  $p\text{-value}=0.0003$ ;  $Q=32.36$ ,  $p\text{-value}=0.0090$ ) (Supplementary  
409 S3; Supplementary S4) while no significant difference was found when comparing  
410 subgroups for infestation rates ( $Q=18.45$ ,  $p\text{-value}=0.1871$ ).

411 High parasitic load estimates were found for small mammals and birds such as  
412 *Emberizidae*, *Leporidae*, *Strigidae*, *Tytonidae* and *Paridae* families. High competitiveness  
413 estimates were found for most of the families except for the *Corvidae* and *Turdidae*.

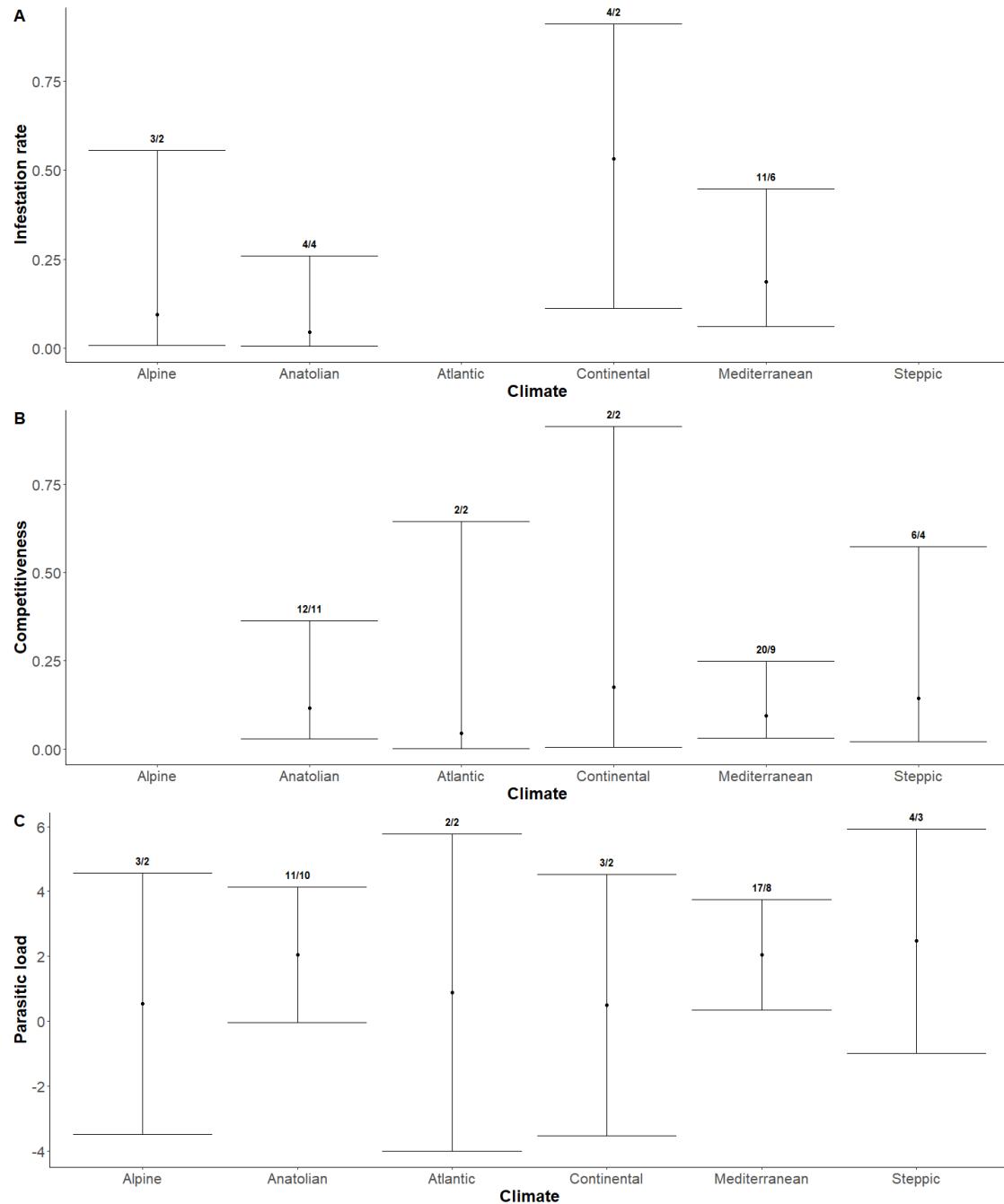
414 Residual heterogeneity  $I^2$  after accounting for host effect was 83.1%, 80%, 86.2% for  
415 infestation rate, competitiveness and parasitic load, respectively.

416

## Landscape effect

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### Adult stage



418

**Figure 9.** Effect of Climate type on (A) infestation rate (B) competitiveness (C) parasitic load for adult stages. Effect size are represented with their 95% confidence intervals. The numbers on top of the error bar correspond to the number of distinct reports of interaction with host against the number of publications

419

420 The 95% confidence interval for pooled values for each effect size were wide (Figure 9). No  
421 significant difference was found between climates regardless of the effect size ( $Q=4.72$ , p-  
422 value=0.1935;  $Q=0.50$ , p-value = 0.9732;  $Q=1.19$ , p-value=0.9460 for infestation rate,  
423

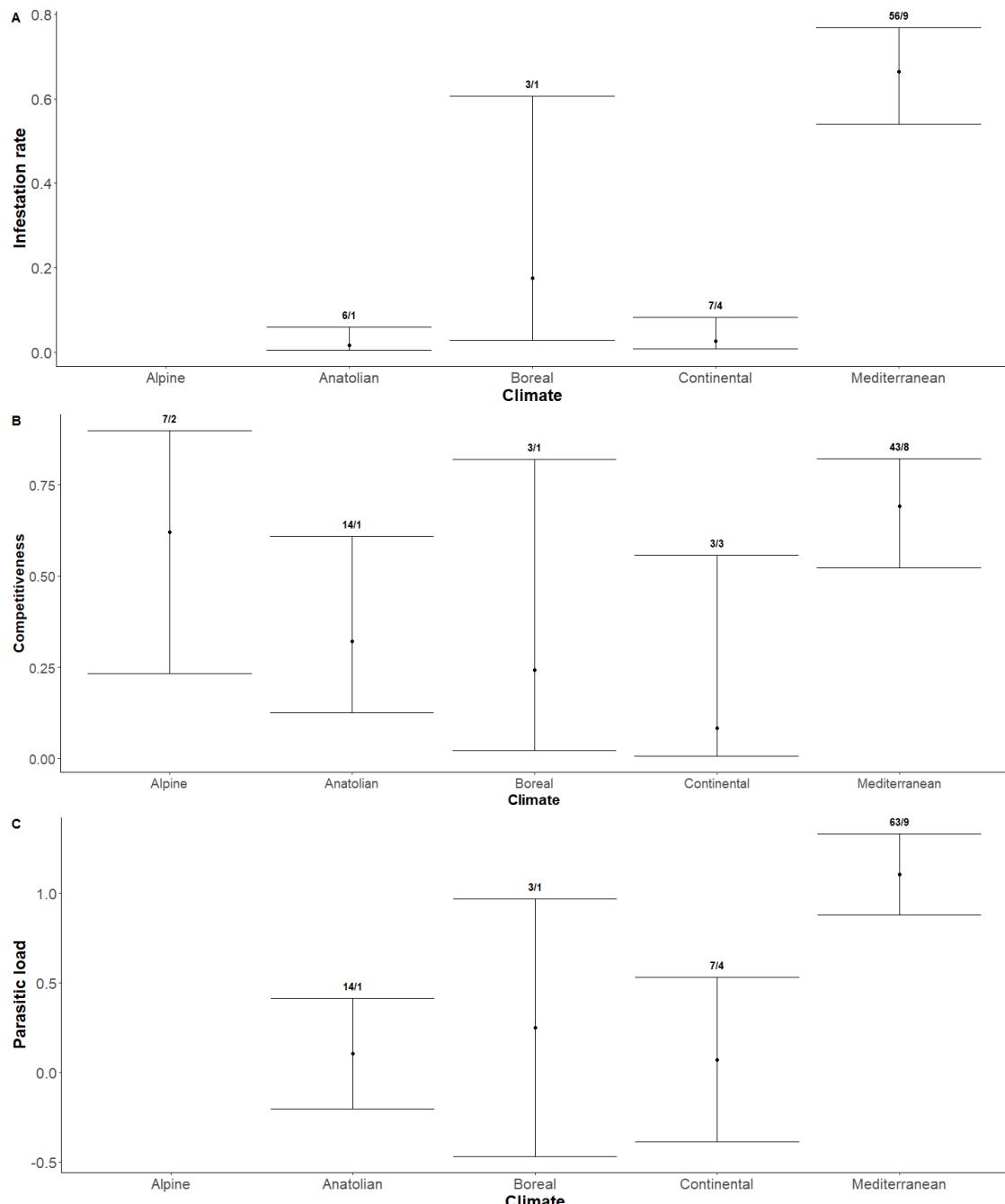
424

425 competitiveness and parasitic load respectively). The highest estimation was found in  
426 Mediterranean and Anatolian climates, except for infestation rate where it was Continental  
427 and Mediterranean. Residual heterogeneity  $I^2$  after accounting for climate was 83.9%, 99.5%,  
428 99.8% for infestation rate, competitiveness and parasitic load respectively.

429

430 **Immature stages**

431



432

433 **Figure 10.** Effect of Climate type on (A) infestation rate (B) competitiveness (C) parasitic load for immature  
434 stages. Effect size are represented with their 95% confidence intervals. The numbers on top of the error bar  
435 correspond to the number of distinct reports of interaction with host against the number of publications

436

437 The 95% confidence interval were wide for pooled value of all effect sizes (Figure 10).

438 Significant differences were found among climates for infestation rate, competitiveness and  
439 parasitic load ( $Q=79$ ,  $p\text{-value}<0.0001$ ;  $Q=10.01$ ,  $p\text{-value}=0.0403$ ;  $Q=138.23$ ,  $p\text{-value}<0.0001$   
440 respectively) (Supplementary S5; Supplementary S6; Supplementary S7).

441 Highest values were found in the Mediterranean climate for all effect sizes.

442 Residual heterogeneity  $I^2$  after accounting for climate was 87.4%, 92%, 71.0% for  
443 infestation rate, competitiveness and parasitic load respectively.

444 **Habitat Suitability effect**

445 **Adult stage**

446 The residual heterogeneity  $I^2$  after adjusting for suitability was 94.8%, 99.90, 100% for  
447 infestation rate, competitiveness and parasitic load, respectively.

448 No significant effect of suitability was detected in adults ticks for infestation  
449 rate, competitiveness or parasitic load.

450 **Immature stages**

451 The residual heterogeneity  $I^2$  after adjusting for suitability was 95.26%, 91.49% and 99.99  
452 % for infestation rate, competitiveness and parasitic load respectively.

453 No significant association was found for infestation rate and parasitic load. Nevertheless,  
454 there was a significant positive association between habitat suitability and competitiveness  
455 during immature tick stages ( $QM = 13.9024$ ,  $p\text{-val}< 0.0001$ ).

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## **Effect of birds behavior on outcomes**

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**Table 4:** Posterior distribution of the mean comparative behavior estimates. G/M correspond to ground feeding or hunting migratory birds; G/NM correspond to ground feeding or hunting non-migratory birds; NG/M correspond to non-ground feeding or hunting migratory birds.

Contrast	Estimate	Conf.low	Conf.high
G/M - G/NM	0.184	-0.042	0.359
NG/M - G/NM	0.187	-0.083	0.439
G/M - G/NM	-0.254	-2.24	0.756
NG/M - G/NM	-0.773	-2.69	0.332
G/M - G/NM	0.093	-0.093	0.244
NG/M - G/NM	0.023	-0.174	0.212

462 Analysis of pairwise marginal effects across various bird behavior values, indicated that  
463 non-migratory species and those species feeding or hunting on the ground showed higher  
464 average levels of infestation rate, parasitic load, and competitiveness. Nonetheless, no  
465 substantial differences were observed between bird behavior classes (Table 4).

466

## **Discussion**

467 A better understanding of the interactions between ticks and their hosts is essential for  
468 population regulation processes and the spread of a tick-borne diseases. This study  
469 explored tick-hosts interactions within the genus *Hyalomma* with a focus on *H. marginatum*.  
470 Most of the publications retrieved from scientific publication databases were published  
471 between 2004 and 2021 suggesting an increased concern with regards to *Hyalomma* and  
472 associated diseases in Europe. A possible explanation for this trend could be related to  
473 climate change and modifications of land use that raise concerns regarding the expansion of  
474 *Hyalomma* ticks in Europe (Gray et al., 2009; Diuk-Wasser et al., 2021). Moreover, most of  
475 these publications referred to regions where CCHF has been documented to actively  
476 circulate such as Turkey, Mediterranean Islands, The Balkans region and Central Europe.

477 The high citation record observed for *H. marginatum* can be explained by the fact that it is  
478 the main vector of CCHF virus in many countries where the disease is endemic such as  
479 Turkey (Bente et al. 2013). Moreover, this tick is also the one for which the largest number  
480 of host species is reported. Nevertheless, it cannot be concluded that *H. marginatum* is the  
481 most generalist tick of its genus as this observation could be an effect of a more important  
482 sampling effort. Indeed, a correlation was observed between the number of distinct host-  
483 tick interactions records (which can be considered as a proxy of sampling effort) and the  
484 number of host species reported. This correlation has also been observed by other authors

485 in the context of literature reviews to assess the link between specificity and sampling  
486 effort (Klompen et al., 1996). Noticeably, *H. rufipes* appeared as an outlier in this  
487 correlation, its number of citations being nearly 5 times lower than for *H. marginatum* but  
488 with almost the same number of host species reported (2/3 of the number for *H.*  
489 *marginatum*), suggesting its generalist character.

490 As expected, a strong heterogeneity among pooled effect sizes was found in the meta-  
491 analysis for all outcomes. Furthermore, as observed in previous systematic reviews, fewer  
492 infested species have been reported for adult stages than for immature stages (Nava and  
493 Guglielmone, 2013). This supports the hypothesis that immature stages are more generalist  
494 than adult ones due to their need to feed on morphologically larger hosts.

495 For adult tick stages, a significant effect of host species on the proportion of *H. marginatum*  
496 ticks infesting a host among all the ticks infesting that host (i.e. competitiveness) was  
497 detected. The effects of host species on the proportion of examined hosts infested by *H.*  
498 *marginatum* (i.e. the infestation rate) and on the average number of *H. marginatum*  
499 infesting the examined hosts (i.e. the parasitic load) were not significant. This can be  
500 explained by the limited number of exploitable records retrieved from the literature for  
501 parasitism effect sizes (resulting in wide 95% confidence intervals for the mean estimations  
502 of each host species). Nevertheless, higher estimates of these effect sizes were obtained for  
503 horses and *Cervidae* than for *Caprinae*, wild boars, hares and to a lesser extent, cattle. The  
504 estimations obtained for *Cervidae* must be considered with caution because the number of  
505 publications reporting values of effect sizes was low. In addition, in one of the publications,  
506 *H. marginatum* could have been confused with *H. lusitanicum* and misclassified. Aside from  
507 estimations for *Cervidae*, results obtained were consistent with one study where horses  
508 were more often and severely infected than cattle, wild boars and domestic goats from the  
509 same area in Corsica (Grech-Angelini et al. 2016).

510 Concerning immature tick stages, a significant variation among host families was detected  
511 for competitiveness and parasitic load with high mean estimations in the cases of rabbits  
512 and bird families (*Emberizidae* *Leporidae*, *Strigidae* and *Paridae*) for both effect sizes.  
513 *Emberizidae* encompass a small family of passerine birds which feed frequently on the  
514 ground, thus favoring contact with *H. marginatum*. On the other hand, high estimates of  
515 parasitism of this tick species were not expected for *Strigidae* and *Paridae* as species  
516 belonging to these families do not typically spend a large amount of time on the ground.  
517 However, estimations obtained for these two families were not particularly robust.

518 Despite record numbers and sample size issues, investigating variations in parasitism effect  
519 sizes at a zoological family level, may generate a certain within-group heterogeneity, since  
520 species belonging to the same zoological family may differ in their ecology and  
521 consequently in their availability and/or suitability as hosts for *H. marginatum*. Indeed, a  
522 strong intra-family heterogeneity translated into a large 95% confidence interval around  
523 the estimate, was observed with large differences in infestation rate or parasite load for  
524 certain species. For example, values of *Muscicapidae* family, ranged between 0.001 and 1.00  
525 reported infestation rates values in the. This high heterogeneity can be partially attributed  
526 to interspecific differences within the family. We hypothesized that immature stages of *H.*  
527 *marginatum* behaved as generalist parasites of small vertebrates, implying that parasitism

528 effect sizes would differ among potential host species, primarily due to differences in their  
529 availability influenced by behavior and habitat. However, our models did not reveal  
530 significant evidence supporting this hypothesis, despite finding higher *H. marginatum*  
531 parasitism estimates for non-migratory birds spending time on the ground, an activity that  
532 enhances host availability. This absence of effect could be explained by the limited  
533 availability of data for modeling and unaccounted confounding factors such as seasonality,  
534 geographical location, and sampling effort.

535 A consistent finding in our meta-analysis presented here is the large heterogeneity  
536 observed in effect sizes of parasitism that remain after adjusting for host species or host  
537 family effects. This suggests that other variables are more important in explaining *H.*  
538 *marginatum* variation in effect sizes than those considered in our study. In this regard, a  
539 substantial amount of heterogeneity was explained by the climate variable for immature  
540 stages with highest estimations obtained for the Mediterranean climate, supporting the  
541 results from previous studies on the drivers of the geographical distribution of *H.*  
542 *marginatum* (Bah et al 2022). Similarly, a positive relationship was found between  
543 immature *H. marginatum* tick competitiveness on hosts and environment suitability as  
544 derived from a statistical model of *H. marginatum* distribution fitted to *H. marginatum*  
545 presence-only data. These results support the hypothesis that the impact of climate might  
546 be more critical to the completion of *H. marginatum* immature stages than the composition  
547 of the potential host community (Cumming 2002; Estrada-Peña et al. 2020; Nava and  
548 Guglielmone 2013).

549 In contrast, in the analyses presented here, neither climate nor environmental suitability  
550 contributed to explaining heterogeneity in parasitism effect sizes for the adult stage except  
551 for the competitiveness rate that had a positive correlation with the environmental suitability  
552 index.

553 The failure to detect significant relationships between parasitism effect sizes and  
554 environmental factors could arise from the failure to record accurate and precise  
555 information on geographical location, the dates of the surveys, the number of examined  
556 animals, the number of infested animals, and the number of ticks collected.

557 Another important limitation for identifying the relative influence of host species and  
558 environmental conditions, was the limited number of recorded data on the effect size of  
559 parasitism available in the identified sources literature for most of the potential host  
560 species or families. Given the large heterogeneity in effect-size values detected in most of  
561 the host species, which are likely to be related to environmental variability, mean estimates  
562 of effect size at species or family level were likely to be imprecise and biased (Borenstein et  
563 al. 2011). Moreover, effects of environmental conditions and host species or family are  
564 exposed to many potential confounding factors.

565 In order to better describe the tick-host relationship of *H. marginatum* using a meta-  
566 analysis approach, more abundant and accurate records of parasitism effect-size would be  
567 required for each potential host species or family. Moreover, in order to avoid confounding  
568 effects, such records should ideally originate from areas where environmental conditions  
569 are contrasted. In this particular context, surveys where ticks are recorded on several host  
570 species in the same area (ideally all the potential host species found in the area) at the same

571 time of year are particularly useful for investigating the empirical variation of infestation  
572 levels among different hosts species. Using this type of approach would be much more  
573 efficient for addressing variation in infestation measures among host species than  
574 controlling for the potential confounding effect of the environment, since each record  
575 considered in the meta-analysis would reflect a difference in an infestation measure  
576 obtained from two different host species under the exact same environmental conditions.

577 In conclusion, our study highlights the relevance of assessing the abundance and diversity  
578 of the host community present in a given location in order to provide an estimation of the  
579 risk of pathogen transmission. From that perspective, our study suggests that *H.*  
580 *marginatum* is a generalist tick whose distribution depends primarily on environmental  
581 conditions such as climate and habitat. Its trophic relationships will therefore be primarily  
582 determined by the hosts community available in its immediate environment. The  
583 circulation of the pathogen will therefore depend on the number of hosts available and their  
584 capacity to replicate and amplify the virus and /or the tick population (Bernard et al. 2022;  
585 Occhibove et al. 2022). Moreover, our analysis highlights the importance of implementing  
586 as precise data collection and information on future surveys of tick species and their hosts  
587 that can be subsequently used for building statistical models to infer information on  
588 complex ecological host-vector pathogen interactions.

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## 595 **Conflict of interest disclosure**

596 The authors declare that they comply with the PCI rule of having no financial conflicts of  
597 interest in relation to the content of the article.

## 598 **Data, scripts, code, and supplementary information**

599 The authors declare that they comply with the PCI rule of having no financial conflicts of  
600 interest in relation to the content of the article.

601 Data, scripts and code are available online: <https://doi.org/10.5281/zenodo.13737782>

602 Supplementary information is available online on biorxiv as part of the preprint.

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