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1 **How general are generalist parasites? The small mammal part of**  
2 **the Lyme disease transmission cycle in two ecosystems in northern**  
3 **Europe**

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15  
16 **Author contributions**

17 AM conceived and designed the study. VMS, AH and HL did the field work. VMS did the  
18 DNA labwork. HL and AH did the tick counting. HV and AM did the statistical analyses and  
19 made the figures. AM drafted the paper. All authors gave comments to the ms. and gave final  
20 approval before submission.

21

22 **Abstract**

23 Generalist parasites face the challenge of how to evade multiple immune defences. Even  
24 generalist parasites may adapt to the primary local host in a given region (host race  
25 formation). We here compare load of *Ixodes ricinus* (the vector) on small mammals and  
26 investigate the infection prevalence of *B. burgdorferi* s.l. (the pathogen) involved in the  
27 enzootic transmission cycle of Lyme disease in two contrasting ecosystems in Norway from  
28 2014-16. The most common larval tick host in the eastern region was the bank vole, while the  
29 common shrew dominated in the western region of Norway. However, the wood mouse and  
30 the bank vole had consistently higher larval tick loads than the common shrew in both  
31 ecosystems. Hence, there was no evidence of host race formation; instead, the evidence  
32 indicated that species are differently suitable as hosts, regardless of their abundances. The  
33 pathogen infection prevalence was similar among small mammal species, but markedly higher  
34 in the region with larger small mammal populations and higher tick loads, while the seasonal  
35 and annual variation was less marked. Our study indicated that the generalist *I. ricinus* shows  
36 consistent patterns of load on species of small vertebrate hosts, while *B. burgdorferi* s.l. (*B.*  
37 *afzelii*) was a true generalist. The similar roles of host species across regions suggest that  
38 disease dynamics can be predicted from host community composition, but predicting the role  
39 of host community composition for disease dynamics requires a detailed understanding of the  
40 different species population limitations under global change.

41 **Keywords:** Lyme borreliosis · transmission cycle · density-dependence · *Borrelia burgdorferi*  
42 · *Ixodes ricinus* · seasonality

## 43 **Introduction**

44 The dynamic processes associated with disease transmission networks have broad ecological,  
45 evolutionary and societal significances (Rigaud et al. 2010; Sexton et al. 2017). Such  
46 community structures vary from a single-host pathogen to multi-host vector-pathogen  
47 structures (Johnson et al. 2015). The complexity of transmission within vector-borne disease  
48 systems increases through interspecific interactions between pathogen-vector and vector-host  
49 in addition to pathogen-host interaction (Estrada-Peña et al. 2015). The coexistence and  
50 relative benefits of being generalist or specialist parasites are the keys to understanding  
51 networks of species within natural disease systems (Woolhouse et al. 2001). It has been  
52 theorized that parasites that are more host-specific will achieve greater numbers on their  
53 respective host, as opposed to generalist parasites, due to the cost of adaptation against  
54 multiple host defence systems. Due to these immune defence costs, even generalist parasites  
55 may adapt to the main local host in a given region, a process termed host race formation  
56 (McCoy et al. 2013). However, these processes also depend on the population dynamics of the  
57 species involved in the vertebrate community, as relative abundances of hosts over time may  
58 affect the trade-offs (Woolhouse et al. 2001), as shown for ectoparasitic fleas (Krasnov et al.  
59 2004).

60 Lyme disease is the most common vector-borne zoonosis in the northern hemisphere, and it  
61 has a particularly complicated transmission (Radolf et al. 2012; Coipan & Sprong 2016).

62 Lyme disease is caused by specific genospecies from within the *Borrelia burgdorferi* sensu  
63 lato complex, and the pathogens are all vectored by generalist tick species from the Ixodidae  
64 family (Franke et al. 2013). These include *I. ricinus* in Europe, west Asia and north Africa, *I.*  
65 *persulcatus* in Asia and eastern Europe, *I. scapularis* in eastern North America and *I.*  
66 *pacificus* in western North America (Franke et al. 2013). The different life stages of the  
67 Ixodidae ticks are found on a wide range of vertebrates; however, it is poorly understood

68 whether spatial variation in host use reflect variations in species distribution causing local  
69 host race formation. The extent to which removal or low abundance of one host species can be  
70 buffered by other species in the vertebrate community depends on whether other species are  
71 equally competent as hosts, which we normally would expect for generalist species by  
72 definition. However, removal of the main larval hosts, western fence lizards (*Sceloporus*  
73 *occidentalis*), in California only led to a marginal redistribution of the assumed generalist *I.*  
74 *pacificus* ticks on other hosts (Swei et al. 2011). Although *I. ricinus* is found on a wide range  
75 of mammals and birds, few species of vertebrates seem to dominate the transmission  
76 dynamics in Europe (Hofmeester et al. 2016). Indeed, the assembly of host communities and  
77 tick-feeding patterns across different habitats is still identified as a current knowledge gap in  
78 Lyme disease (Kilpatrick et al. 2017). The host selection of vectors greatly impacts  
79 epidemiology (Gandon 2018). Therefore, we need to know tick burdens, both relative and  
80 absolute, on different species across a range of host communities and abundances (Kilpatrick  
81 et al. 2017); however, such empirical studies are rare (Krasnov et al. 2007).

82 Rodents infect most *I. ricinus* larvae (89 %) with *B. burgdorferi* s.l. in Europe (Hofmeester et  
83 al. 2016). The small mammal species involved in transmission may differ regionally  
84 (Kilpatrick et al. 2017), but this insight is based on few studies, often single-year studies with  
85 small sample sizes. Small mammal-transmitted *B. burgdorferi* s.l. (mainly *B. afzelii*) are  
86 thought to be maintained due to the high density of their reservoir hosts (Hofmeester et al.  
87 2016), but whether population density of the reservoir hosts affect high *B. burgdorferi* s.l.  
88 prevalence has been rarely quantified. In northern environments, there is substantial annual  
89 variation and often cyclic dynamics of small mammals (Bjørnstad et al. 1995; Ims &  
90 Andreassen 2000). Such dynamics may or may not be synchronous between species, which  
91 may affect the stability of the resource base to ticks. Furthermore, several studies have  
92 indicated an important role of shrews in feeding tick larvae (Brisson et al. 2008; Bown et al.

93 2011; Mysterud et al. 2015), and shrews are insectivores in contrast to rodents. Abundances of  
94 shrews are sometimes but not always linked to the rodent cycles by shared predation (Strann  
95 et al. 2002; Korpimäki et al. 2005), which may have implications for disease dynamics (Ecke  
96 et al. 2017). Furthermore, ticks are expanding their distribution towards northern latitudes  
97 (Jore et al. 2011; Medlock et al. 2013), leading to the emergence of Lyme disease (Mysterud  
98 et al. 2016; Mysterud et al. 2017; Sajanti et al. 2017). This emergence poses an interesting  
99 setting to understand how tick populations and *B. burgdorferi* s.l. infections are limited by  
100 small mammals.

101 We here analyse the load of *I. ricinus* and *B. burgdorferi* s.l. infection prevalence in a large  
102 sample of 1,659 individuals from 9 different small mammal species over three years (2014-  
103 16) in two contrasting regions (ecosystems) of Norway. One of the regions ('west') has a high  
104 incidence of Lyme disease in humans, while the other region ('east') has a relatively low  
105 incidence of Lyme disease (Mysterud et al. 2016) and of other tick-borne diseases (Mysterud  
106 et al. 2017; Mysterud et al. 2018b). In both regions, the wood mouse (*Apodemus sylvaticus*),  
107 the bank vole (*Myodes glareolus*) and the common shrew (*Sorex araneus*) are quite abundant,  
108 enabling a comparative analysis of relative tick load and infection prevalence between the two  
109 contrasting regions. The eastern region is dominated by the bank vole, while the western  
110 region is dominated by the common shrew. We aimed to determine the extent to which these  
111 species are equally competent as hosts to ticks (i.e., no difference in innate immunity), and we  
112 used infection prevalence as a proxy for transmission competence of the pathogen *B.*  
113 *burgdorferi* s.l. causing Lyme disease. We acknowledge that infection is not the same as host  
114 or vector competence (Bockenstedt et al. 2002), which is required for transmission. However,  
115 we elsewhere present evidence that all sequences come from *B. afzelii* (Mysterud et al.  
116 2018a), a genospecies known to be transmission competent in several small mammal species  
117 (Gern et al. 1998). We aimed to test the predictions from hypotheses reviewed in table 1

118 related to (1) species competence as hosts and whether this competence depends on the small  
119 mammal species composition of the ecosystem. We determined whether the relative  
120 abundance of ticks on small mammal hosts are variable between regions and years, or are  
121 relative abundances higher on the more abundant host, as would be expected if there was host  
122 race formation? We also tested (2) whether tick load and infection prevalence are density  
123 dependent at seasonal and annual scales due to dilution or linked to spatial variation in the  
124 population density of hosts across the two regions (Table 1). Finally, we expected that the  
125 infection prevalence would be linked to nymphal rather than larval tick load (Coipan &  
126 Sprong 2016). The literature is unclear as to whether the pathogen survives in the tick  
127 (Tälleklint & Jaenson 1995) or reservoir host (Gern et al. 1994a) during the winter. If the  
128 pathogen survives in the tick only during winter, we would predict lower infection levels in  
129 small mammals in spring relative to fall.

## 130 **Materials and methods**

### 131 **Study areas**

132 *East.* The eastern study area is located in the Vestby municipality, Akershus county of  
133 Norway. The landscape morphology and topology in the region are characterized by low  
134 variation in elevation, with the trapping stations ranging from 58 to 137 m a.s.l. Although  
135 close to the coast of the Oslofjord, the climate is quite dry, with an average annual  
136 temperature of 3.4°C and average total precipitation of 735 mm (Norwegian meteorological  
137 station no. 03780, met.no). Vestby is situated in the geological area named the Oslo field  
138 (“Oslofeltet”). The bedrock here mostly consists of gneisses. The vegetation is classified as  
139 part of the boreonemoral zone (Abrahamsen et al. 1977), and dominant coniferous tree species  
140 are either Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*). The deciduous forests  
141 are dominated by birch (*Betula* spp.) or oak (*Quercus robur*), with elements of alder (*Alnus*

142 *incana*), goat willow (*Salix caprea*), hazel (*Corylus avellana*) and aspen (*Populus tremula*),  
143 and a mix of grasses, shrubs and herbaceous plants covering the field layer. Forests are  
144 managed for forestry purposes, and there are many agricultural fields, primarily growing  
145 grains.

146 *West*. The western study area is in the Askvoll and Førde municipalities in Sogn & Fjordane  
147 county, Norway. The topography is characterized by steep mountain hills and valleys, with  
148 rivers and streams. The elevation among the trapping stations ranges between 11 and 355 m  
149 a.s.l. The climate is coastal, with cool summers and mild winters and an average temperature  
150 of 6°C and yearly precipitation of 2270 mm (Norwegian meteorological station no. 57170).  
151 The bedrock is mostly dominated by gneiss, granite and other plutonic rock types. The area is  
152 situated within the boreonemoral zone (Abrahamsen et al. 1977). The vegetation primarily  
153 consists of mixed forests with deciduous woodland dominated by birch at higher elevations  
154 and alder at lower elevations. The field layer is dominated by grasses, with a mix of  
155 herbaceous plants. Other parts consist of coniferous forests, usually dominated by Scots pine  
156 and areas of planted with Norway spruce. There are agricultural fields at lower elevation,  
157 primarily growing grass for livestock winter fodder. For further details, see cfr. (Myserud et  
158 al. 2018b).

159

### 160 **Capturing of small mammals**

161 We captured small mammals in the spring and fall from 2014-2016 from the western and  
162 eastern regions of Norway. The tick load data from 2014 in western Norway has been  
163 previously presented (Myserud et al. 2015). The traps were set and baited the first day, and  
164 then checked for three consecutive days in each season. In western Norway, we had 50  
165 trapping stations, with a total of 200 traps. In eastern Norway, we had 25 trapping stations,

166 with a total of 100 traps. Since the ‘west’ region have double the amount of traps as the ‘east’  
167 region, our reference to abundances is capture numbers taking this into account.

168 The trapping stations had a minimum distance of minimum 500 m from one another to avoid  
169 local depletion of populations. For logistic reasons, all trapping stations were situated in  
170 proximity to roads, with a minimum distance of 50 m away from roads. At each trapping site,  
171 four traps were placed in the corners of a 15×15 m square, according to the small quadrat  
172 method (Myllymäki et al. 1971). The traps are positioned in the terrain to maximize the  
173 probability of capture within 2 m of each corner. The trap coordinates and elevations were  
174 collected using a handheld GPS.

175 The traps used were “Ugglan”-traps from Grahnab, which are live traps, in which the animals  
176 are caught within a small cage. The trap were covered with a metal sheet to protect the  
177 animals from the weather and to keep predators away. They were baited with oats for food  
178 and a piece of carrot for water to sustain the animals before the traps were emptied. The small  
179 mammals that were caught, were culled by cervical dislocation and then stored in individual  
180 closed zip-lock bags to prevent the ticks from escaping. The bags were marked with an  
181 individual number, trap number and date of capture before they were stored in a freezer for  
182 later examination in the laboratory.

### 183 **Species identification of small mammals and ticks**

184 In the lab, the animals were weighed, determined to species and examined for ticks. Each  
185 animal was defrosted before being examined under a magnifying glass, using a tweezer to  
186 locate and remove on-host ticks. The set standardized time for examining each small mammal  
187 individual was 20 minutes. This time was set to ensure that each animal was given the same  
188 level of examination and based on the experience from an earlier, similar study (Mysterud et  
189 al., 2015). Typically, few ticks were found in the last five minutes of the examination, except



190 in rare cases, and this time limit is unlikely to yield bias, even though the surface areas differ  
191 between species. Ticks that dropped off in the sealed bags were included. Species  
192 determination of small mammals was performed either by external morphological  
193 characteristics (shrews and *Apodemus* sp.) or by examination of teeth (*Microtus agrestis* and  
194 *Myodes glareolus*). An expert on small mammals checked all our species identifications  
195 (Jeroen van der Kooij). During examination, the ticks were removed from the animal and  
196 placed aside for identification. After removal, the ticks were counted and identified by species  
197 and developmental stage (larvae, nymph or adult) under a stereomicroscope using  
198 morphological characters. A tissue sample from each animal's ear was collected to be used in  
199 pathogen detection.

## 200 **Pathogen determination**

201 We used an established qPCR protocol (Allender et al. 2004), implemented at our lab (CEES)  
202 to determine presence of *B. burgdorferi* s.l. in ear tissue from small mammals (Mysterud et al.  
203 2013; Mysterud et al. 2016). This method uses multiplex real-time PCR with a Roche  
204 Lightcycler® 96 instrument (Courtney et al. 2004).

## 205 **Statistical analyses**

206 Statistical analyses were performed in R (R Development Core Team 2016). We analysed the  
207 load of *I. ricinus* tick larvae with negative binomial models in library glmmADMB (Skaug et  
208 al. 2006), while we analysed *B. burgdorferi* s.l. with a mixed effects logistic regression  
209 models in library lme4. In both areas, the wood mouse, bank vole and common shrew were  
210 numerous, while the remaining small mammal communities differed regionally (Fig. 1).  
211 Therefore, we restricted our analysis to these three species to allow for regional interaction  
212 terms. Factor variables were small mammal species (3 levels), year (as 3 levels), season  
213 (spring/fall) and their interactions, while trapping station was included as a random term. A

214 variable notifying the status of common shrews when captured (3 levels: not recorded, dead or  
215 live) was also included. We used the Akaike Information Criterion (AIC) and Bayesian  
216 Information Criterion (BIC) for model selection. We primarily relied on the more  
217 conservative BIC when the criteria did not provide the same results, as we were interested in  
218 the most important quantitative factors. We used the main parameters as a baseline model and  
219 then a forward selection procedure for the interactions. We checked the models using standard  
220 diagnostic tools.

## 221 **Results**

### 222 **The small mammal community**

223 In the eastern region, the total catch was 266 in 2014, 180 in 2015 and 314 in 2016 with 100  
224 traps (Fig. 1). Overall, the bank vole was a common species in the catch in 2014 (38.7%) and  
225 2015 (33.9%), but it was only the most common catch in 2016 (53.8%). The common shrew  
226 dominated in 2014 (41.7%) and 2015 (47.8%) but was lower in proportion in 2016 (23.9%).  
227 Hence, the shrew dynamics were more stable across years and proportion in catch, driven  
228 more by variations in bank vole numbers. In the western region, the total catch was 360 in  
229 2014, 201 in 2015 and 351 in 2016 with 200 traps. The common shrew dominated the catch  
230 for all years, with 49.4% in 2014, 56.2% in 2015 and 58.4% in 2016; hence, the proportion  
231 was unrelated to the total catch (Fig. 1). A descriptive overview of infestation prevalence of  
232 larval ticks (Table S1), larval tick infection intensity (Table S2), and infection prevalence of  
233 *B. burgdorferi* s.l. (Table S3) for all the species is given in the Supporting Information.

### 234 ***I. ricinus* larval load**

235 The best model of larval tick load (Table S4), restricted to the three most common species,  
236 included the species, region, season, year, the interaction terms “season\*year”, “region\*year”  
237 and “region\*year\*season”, in addition to a variable accounting for whether the common

238 shrew was dead or alive at capture (Table 2). The sequence rank of species was therefore  
239 consistent across regions and years, with the wood mouse and the bank vole having higher  
240 individual load than the common shrew (Fig. 2). There was a marked effect of region, with  
241 consistently higher larval tick loads in the eastern Norway compared to western Norway. This  
242 finding was due to the combination of infestation prevalence (Table S1) and intensity (Table  
243 S2), with a tendency for the wood mice to have lower infestation prevalence, but higher  
244 infestation intensity than the bank vole. However, adding a zero inflation term, which in  
245 theory can tease apart infestation prevalence and intensity, did not improve model fit. The  
246 difference across years was larger in the western ecosystem than the eastern ecosystem (Table  
247 2, Fig. 2). Tick loads were usually higher in spring than in fall (Table 2). There was a lower  
248 tick load on dead shrews compared to live shrews, but this did not affect the ranking of  
249 species.

#### 250 ***I. ricinus* nymphal load**

251 The best larval tick load model included species, season, and region, with no interaction terms  
252 (Table S4). The nymphal load was higher in the wood mice and the bank vole than for the  
253 common shrew; the load was higher in the east than in the west and higher in the spring than  
254 in the fall (Table 3).

#### 255 ***B. burgdorferi* s.l. infection prevalence**

256 The infection prevalence of *B. burgdorferi* s.l. varied as a function of region, year, season  
257 nymphal load and the interaction term “season\*nymphal load” (Table S5), while there was no  
258 significant difference between species (Table 3, Table S3). The infection levels were much  
259 higher in the east (23 – 48 %) compared to the western (5 – 10 %) region of Norway (Fig. 3).  
260 The higher infection prevalence in 2016 was driven by a peak in the east region; however, the  
261 data set was not sufficiently large for an interaction between region and year to enter the most  
262 parsimonious model. There was higher infection prevalence in spring than in fall, probably

263 due to higher nymphal load in spring. After accounting for season, there were higher infection  
264 levels in the autumn, with increasing nymphal load.

## 265 **Discussion**

266 Disease ecology is still in the process of being blended with community ecology (Johnson et  
267 al. 2015). The level of niche breadth in host use of different species, i.e. their level of  
268 specialization, is an old theme in ecology to understand community networks (Futuyma &  
269 Moreno 1988; Sexton et al. 2017) and important to understanding transmission dynamics in  
270 our case (Woolhouse et al. 2001). Generalist parasite species are often defined by their host  
271 use across their distribution range, which can ignore important specialization of a species to  
272 the local host community (Bolnick et al. 2003). For the generalist Ixodes ticks, knowing the  
273 answer to the extent to which host specialization occur has important implications for the  
274 transmission of Lyme disease (McCoy et al. 2013). In general, there is a restricted number of  
275 vertebrate species that dominate as hosts for *I. ricinus* in Europe (Hofmeester et al. 2016);  
276 however, the dominant small mammal hosts to tick larvae may vary geographically  
277 (Kilpatrick et al. 2017). We compared the load of *I. ricinus* larval and nymphal ticks on  
278 common small mammal host species in two contrasting ecosystems. Here, we provide  
279 evidence that although there were significant regional and annual variations in the larval load  
280 across the dominant small mammal species, the relative abundances across species were  
281 consistent (Fig. 2). In contrast, the *Borrelia* infection levels were similar across species but  
282 widely different between the two regions in Norway (Fig. 3). High regional population  
283 abundances of small mammals was linked to markedly higher tick load and resulting  
284 infestation prevalence, while temporal variation at seasonal and annual scales was smaller.

## 285 **The generalist tick with preferences: the same host is always better**

286 Generally, there is good understanding of the broad picture of the Lyme disease transmission  
287 cycle (Franke et al. 2013; Coipan & Sprong 2016). However, we know little about how the  
288 host use of the generalist tick varies depending on local mammal community composition  
289 (Kilpatrick et al. 2017). There are surprisingly few studies of host use at northern latitudes of  
290 Europe; existing studies have limited sample sizes (Tälleklint & Jaenson 1997; Paulauskas et  
291 al. 2008). In a recent review (Hofmeester et al. 2016), 29 papers in Europe reported the bank  
292 vole as a host to *I. ricinus* ticks, 22 studies the wood mouse and 21 studies the yellow-necked  
293 mouse, while only 4 papers reported loads on the common shrew. In our study, the bank vole,  
294 the wood mouse and the common shrew were the dominant species, accounting for 69.4% of  
295 the catch in the west and 92.8% in the east (Table 2, Fig. 1). However, their relative  
296 abundances differed between the regions. The common shrew accounted for 79.1% in the  
297 west and 38.8% in the east, while the bank vole accounted for 9% in the west and 47.5% in  
298 the east for this subset of the 3 main species. Eastern and western Norway have different  
299 mitochondrial genotypes of *I. ricinus* ticks, suggesting a 5000-year-old difference (Røed et al.  
300 2016). There has thus been time for local host race formation. Our analysis shows a stable  
301 relative ranking of larval *I. ricinus* tick loads across these hosts, which suggests limited host  
302 race formation and a stable host selection across the two ecosystems and supports a strong  
303 role of innate immunity among the small mammal hosts (Table 1).

304 The distribution range of *I. ricinus* in Europe (Medlock et al. 2013) and *I. scapularis* in  
305 Canada (Gasmi et al. 2016; Clow et al. 2017) is extending towards northern latitudes. For  
306 ticks, this extension will involve a shift in the small mammal communities, with higher annual  
307 fluctuation in their population abundances. The yellow-necked mouse is common in  
308 continental Europe, while the wood mouse is more common towards northern Europe.  
309 However, even the wood mouse is typically limited to southern Norway and Sweden. The

310 bank vole and common shrew have a wider geographical distribution in northern Norway,  
311 Sweden and Finland. For Finland, the bank vole is clearly a dominating species as a host for  
312 ticks (Cayol et al. 2017). In addition to the common shrew, we are the first to report the taiga  
313 shrew (*S. isodon*) as an important tick host and potentially a transmission host for *B.*  
314 *burgdorferi* s.l. The taiga shrew was surprisingly abundant in the western region of Norway.  
315 The taiga shrew was earlier considered to be rare in Norway and is Red Listed as data  
316 deficient (van der Kooij & Solheim 2002), while it is more common in Finland and towards  
317 the east (Hanski & Kaikusalo 1989).

318 The number of larvae on hosts does not directly measure successfully fed larvae, which is a  
319 limitation of our study and most other studies on the subject (Hofmeester et al. 2016).  
320 Tälleklint and Jaenson (1997) found no difference in the proportions of viable nymphs  
321 resulting from larvae engorged on mice or voles, but grooming or acquired immunity may  
322 cause species differences in suitability as hosts to ticks (van Duijvendijk et al. 2016). The  
323 bank vole is known to have acquired immunity, while the yellow-necked mouse does not  
324 (Dizij & Kurtenbach 1995). If acquired immunity is restricted to the bank vole, we would  
325 expect an interaction between small mammal species and season (i.e., a decrease in number of  
326 ticks on the bank vole only from spring to fall), which was not the case with the current  
327 sample sizes, suggesting that the effect was small.

### 328 **The specialized small mammal *B. afzelii*: a generalist on small mammals**

329 Pathogens and their vectors may differ in what limits their host range and level of  
330 specialization (Estrada-Peña et al. 2015). For pathogens, these factors are typically linked to  
331 the phylogeny of their potential hosts rather than their vectors (Kurtenbach et al. 2002). Hosts  
332 can be viewed as different niches to *B. burgdorferi* s.l. (Brisson & Dykhuizen 2004).  
333 Patterns of host-specificity of the *B. burgdorferi* s.l. group are well known at a broad  
334 taxonomic level (Franke et al. 2013), in some cases down to the molecular detail (Kurtenbach

335 et al. 1998; Kurtenbach et al. 2002; Kraiczy 2016). In Europe, *B. afzelii* is the most common  
336 pathogen and linked to a small mammal reservoir, while *B. garinii* is linked to a bird reservoir  
337 together with the less pathogenic *B. valaisiana*. In Europe, *B. burgdorferi* s.s. is most often  
338 transmitted by squirrels (Coipan & Sprong 2016). The genospecies *B. spielmanii* in dormice  
339 and hedgehogs (*Erinaceus europaeus*) and *B. bavariensis* in small mammals and hedgehogs  
340 are also implicated for Lyme disease but have not been reported in Norway and were not  
341 found in a large sample from our study site (Mysterud et al. 2018a). Hence, small mammals  
342 are usually infected with *B. afzelii* in northern Europe, and studies have shown limited host  
343 specialization within the small mammal group for *B. afzelii* (Råberg et al. 2017). Consistent  
344 with these findings, we also found an even infection prevalence of *B. burgdorferi* s.l. across  
345 the dominant small mammal hosts.

346 *B. burgdorferi* s.l. have been suggested to survive the winter in the tick rather than in the  
347 (bank vole) vertebrate transmission hosts (Tälleklint & Jaenson 1995), but *Apodemus* spp.  
348 showed long-term infections in the lab (Gern et al. 1994b). Infected nymphs in the spring re-  
349 infect the vertebrate hosts. Nymphal burdens of host species were linked to infection  
350 prevalence with *B. burgdorferi* s.l. (Hofmeester et al. 2016), as was the case in our study.  
351 Nevertheless, there were similar infection levels across species within region and a large  
352 contrast between the two regions. The most important mammalian reservoirs in south Sweden  
353 were the common shrew and the rodents bank vole, field vole, yellow-necked mouse, and  
354 wood mouse, accounting for 91% of all *I. ricinus* larvae infected (Tälleklint & Jaenson 1994).  
355 In areas without rodents, hares can also maintain *B. burgdorferi* s.l. (Tälleklint & Jaenson  
356 1993). The disease hazard is the density of infected nymphs (Ostfeld et al. 2006), which is a  
357 function of a fraction of larvae that feed on infected hosts and the reservoir and vector  
358 competence of the vertebrate hosts (Kilpatrick et al. 2017). Thus, the contribution of different  
359 small mammal species to the disease hazard are linked to the variation in larval tick load more

360 than to variation in *Borrelia* infection prevalence. For Puumala virus, the ratio of voles to  
361 shrews affected infection prevalence of the different small mammal species (Ecke et al. 2017),  
362 while we found no such dilution effect among these small vertebrate hosts, which appeared to  
363 be equally competent.

#### 364 **The small mammal population dynamics, infection prevalence and disease hazard**

365 We highlight the different mechanisms of how temporal and spatial variation in population  
366 abundances of small mammals may affect components of disease hazard differently (Table 1).  
367 The higher infection prevalence in spring at low population abundance is consistent with a  
368 dilution effect coming from new (non-infected) offspring being recruited into the small  
369 mammal populations towards fall. However, the main finding of our study is that regional  
370 variation in population abundances of small mammals was much more important for both  
371 larval load and infection prevalence compared to effects of seasonal and annual variation in  
372 population abundances. This contrasts for example the dynamics of tularemia caused by the  
373 pathogen *Francisella tularensis*, for which outbreaks were linked to high rodent population  
374 density in a given year (Luque-Larena et al. 2017). A common feature for many directly  
375 transmitted diseases is density-dependent transmission. Likely, the absence of marked effect  
376 of temporal variation in population abundances on infection prevalence may be linked to time  
377 lags in the tick life cycle. Also the flea-borne pathogen *Yersinia pestis* causing plague has  
378 density-dependent outbreaks (Davis et al. 2008), so the level of density-dependent  
379 transmission may differ depending on details of the vector biology.

380 The capacity for explosive growth of rodent populations and their near-ubiquitous presence is  
381 why rodents are marked not only as an important reservoir for zoonotic diseases today but  
382 also as likely candidates for future ones (Han et al. 2015). We are still far from a complete  
383 knowledge of how small mammal communities will affect Lyme disease hazards across



384 Europe, and the small mammal population dynamics are also currently changing (Cornulier et  
385 al. 2013). The similar roles of species across regions suggest that disease dynamics to some  
386 extent can be predicted from host community composition. The ratio of small mammal hosts  
387 available will depend on latitude, with a diminishing number of wood mice and increasing  
388 proportion of bank voles and common shrews. The abundance of field voles has been linked  
389 to climate change (Cornulier et al. 2013), while the numbers of bank voles, wood mice and  
390 common shrews are, to a larger degree, affected by land use (Zarybnicka et al. 2017) and  
391 beech masts (Imholt et al. 2017). Predicting the role of host community composition for  
392 disease dynamics requires a detailed understanding of the different species population  
393 limitations under global change.

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398 **Author contribution statement** AM conceived and designed the study. VMS, AH and HL  
399 did the field work. VMS did the DNA labwork. HL and AH did the tick counting. HV and  
400 AM did the statistical analyses and made the figures. AM drafted the paper. All authors gave  
401 comments to the ms. and gave final approval before submission.

## 402 **Compliance with ethical standards**

403 **Ethical approval** Permissions to capture of rodents and shrews were given by the Norwegian  
404 Environment Agency (reference 2013/11201) and hence conform to the Norwegian laws and  
405 regulations.

406 **Data accessibility** Data will be deposited in Dryad upon acceptance.

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597 **Table 1** An overview of hypotheses and predictions and their links to parameters and conclusions, based on analysis of data over 3 years (2014-  
 598 16) in two contrasting ecosystems (east and west) of Norway. Population abundances are higher in the east compared to the west region.

Hypothesis [scale]	Rationale and prediction	Parameter of interest (direction of estimate)	Reference	Conclusion - tick load	Conclusion - Pathogen infection prevalence
<b>Species host competence</b>					
Equally competent host hypothesis	As expected for a true generalist	No effect 'Species'		Not supported	Supported
Partly competent host hypothesis [temporal]	If generalist with host preferences	'Species': 'year' (more on the most common host species across years)	(Swei et al. 2011) (for <i>I. scapularis</i> )	Not supported. Interaction terms significant, but ranking of species not consistent towards most abundant host	Not supported
Host race formation hypothesis [spatial]	Depending on the abundance a given year; if low abundance of main hosts, higher abundance of alternative hosts	'Species': 'region' (with reversal of species rank towards more common host species across regions)	(McCoy et al. 2013)	Not supported. Interaction terms significant, but similar relative ranking of species	Not supported.
The innate immunity hypothesis [spatiotemporal]	Species have innate different competence as hosts	'Species' without interactions year or region (Bank vole > wood mice for		Supported. Interactions terms significant, but did not affect species ranking	Not supported.

		<i>Borrelia</i> , the opposite for ticks)			
The acquired immunity hypothesis [temporal]	Bank vole has acquired immunity, wood mice do not	'Species': 'season'	(Dizij & Kurtenbach 1995)	Not supported.	Not supported.
<b>Density dependence</b>					
Density dependence [spatial - regional]	More hosts → more ticks → higher infection prevalence	'Region' (higher prevalence in region with higher host density)		Supported (higher east than west)	Supported (higher east than west)
Positive density dependence [temporal - annual]	More hosts → higher infection prevalence	'Year' (higher prevalence in years of higher host density)		Not supported	Not supported
Dilution effect (negative density dependence) [temporal - annual]	More hosts → fewer ticks per hosts → lower infection prevalence	'Year' (lower prevalence in years with higher host density)		Not supported.	Supported east (ambiguous west)
Density-dependent habitat selection of hosts [spatiotemporal]	Hosts are more spread out at higher densities → fewer ticks → lower infection prevalence	'Year' (higher load in years of lower host abundance)		Supported west, not in east	Not supported.
Dilution effect (negative density dependence) [temporal - seasonal]	Recruitment of new juvenile hosts → fewer ticks per host →	'Season' (lower prevalence in fall with higher host density)		Supported.	Supported.

	lower infection levels			
<b>Pathogen winter survival</b>	Pathogen dies in host → lower infection levels in spring	'Season' (higher prevalence in fall as more hosts re-infected after winter)	Not supported.	Not supported.

599

600 **Table 2** An overview of sample sizes of small mammals from western (Sogn & Fjordane  
601 county) and eastern (Akershus county) Norway. Note that “trapping effort” is 200 traps in  
602 western Norway and 100 traps in eastern Norway.

Region		2014		2015		2016		sum
Species	Latin name	spring	fall	spring	fall	spring	fall	
Western								
Yellow-necked mouse	<i>Apodemus flavicollis</i>	3	8	0	2	0	6	19
Wood mouse	<i>Apodemus sylvaticus</i>	5	22	2	6	9	29	73
Field vole	<i>Microtus agrestis</i>	2	19	2	9	0	6	38
House mouse	<i>Mus musculus</i>	0	0	0	0	0	1	1
Bank vole	<i>Myodes glareolus</i>	6	23	2	7	2	18	58
Water shrew	<i>Neomys fodiens</i>	0	5	0	1	0	8	14
Common shrew	<i>Sorex araneus</i>	5	173 <sup>1</sup>	15	98	8	198	497
Taiga shrew	<i>Sorex isodon</i>	1	48	11	41	0	56	157
Pygmy shrew	<i>Sorex minutus</i>	2	32	3	2	1	8	48
Sum		24	330	35	166	20	330	905
Eastern								
Wood mouse	<i>Apodemus sylvaticus</i>	1	27	11	5	15	37	96
Bank vole	<i>Myodes glareolus</i>	22	81	14	47	44	125	333
Water shrew	<i>Neomys fodiens</i>	0	0	1	0	0	0	1
Common shrew	<i>Sorex araneus</i>	3	108	9	77	1	74	272
Pygmy shrew	<i>Sorex minutus</i>	0	22	2	14	1	14	53
Sum		26	238	37	143	61	250	755

<sup>1</sup> Note that the sample sizes differ for *S. araneus* in 2014 relative to (Mysterud et al. 2015) , due to a misclassification of *S. isodon*, which was not known to occur in the area.

603 **Table 3** Estimates from the best model of *I. ricinus* (A) larval and (B) nymphal load and (C)  
604 infection prevalence of *B. burgdorferi* s.l. (*B. afzelii*) in small mammals in eastern and  
605 western Norway from 2014-16. The baseline for the species is the common shrew, and the  
606 status at capture is unknown.

Parameter	Estimate	Std. Error	z	P
<b>A. Larval load</b>				
Intercept	0.654	0.170	3.85	<0.001
Species bank vole	0.422	0.111	3.79	<0.001
Species wood mouse	0.633	0.142	4.44	<0.001
Region east vs. west	0.980	0.263	3.72	<0.001
Season spring vs. fall	-0.804	0.370	-2.17	0.030
Year 2015 vs. 2014	-0.885	0.236	-3.76	<0.001
Year 2016 vs. 2014	-0.655	0.186	-3.52	<0.001
Status at capture (live)	0.078	0.285	0.27	0.785
Status at capture (dead)	-0.480	0.165	-2.91	0.004
Season spring:year 2015	1.345	0.512	2.63	0.009
Season spring:year 2016	2.897	0.472	6.14	<0.001
Region east:year 2015	0.870	0.275	3.17	0.002
Region east:year 2016	0.752	0.189	3.98	<0.001
Season spring:region east:year 2014	1.138	0.441	2.58	0.010
Season spring:region east:year 2015	0.387	0.416	0.93	0.352
Season spring:region east:year 2016	-1.781	0.342	-5.20	<0.001
<b>B. Nymphal load</b>				
Intercept	-3.916	0.300	-13.07	<0.001
Species bank vole	1.211	0.268	4.51	<0.001
Species wood mouse	1.452	0.314	4.62	<0.001
Region east vs. west	1.215	0.322	3.78	<0.001
Season spring vs. fall	1.237	0.251	4.92	<0.001
<b>C. Infection prevalence</b>				
Intercept	-2.935	0.233	-12.59	<0.001
Region east vs. west	1.387	0.232	5.97	<0.001
Year 2015 vs. 2014	0.616	0.215	2.87	0.004
Year 2016 vs. 2014	0.316	0.193	1.64	0.101
Season spring vs. fall	0.477	0.217	2.20	0.028
Nymphal load	1.038	0.196	5.30	<0.001
Season spring:Nymphal load	-0.998	0.230	-4.33	<0.001

607

608 **Figure captions**

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610

611 **Fig. 1** The abundance of small mammal hosts as a function of species, year and region in  
612 Norway. Note that the sampling effort was twice in the west compared to the east.

613

614 **Fig. 2** The predicted mean load of *Ixodes ricinus* larva on small mammal hosts as a function  
615 of species, season, and the year for the eastern and western regions in Norway.

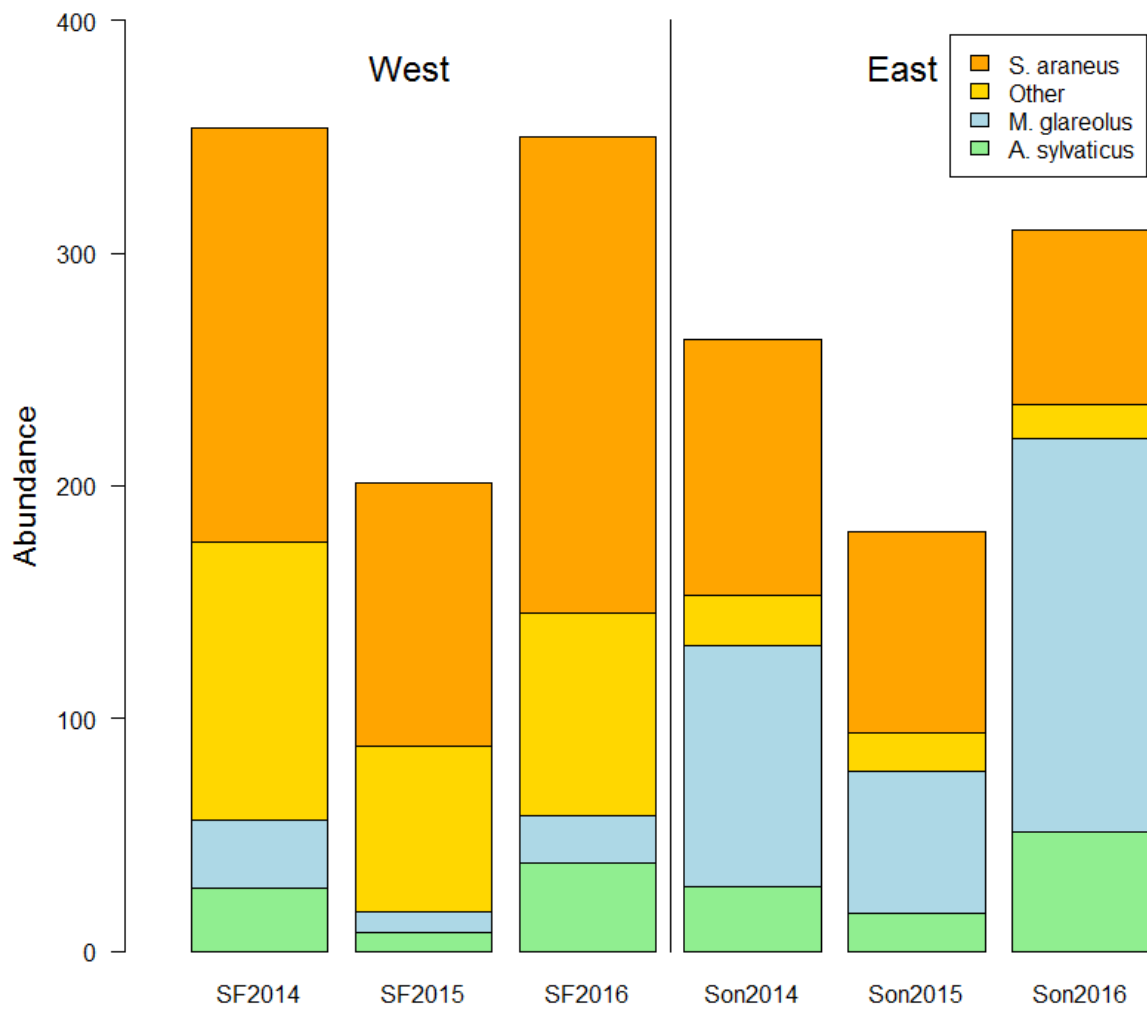
616

617 **Fig. 3** The *Borrelia* infection prevalence per season and year for the eastern and western  
618 regions in Norway. The predicted values are adjusted for the mean number of nymphs per  
619 season and region.

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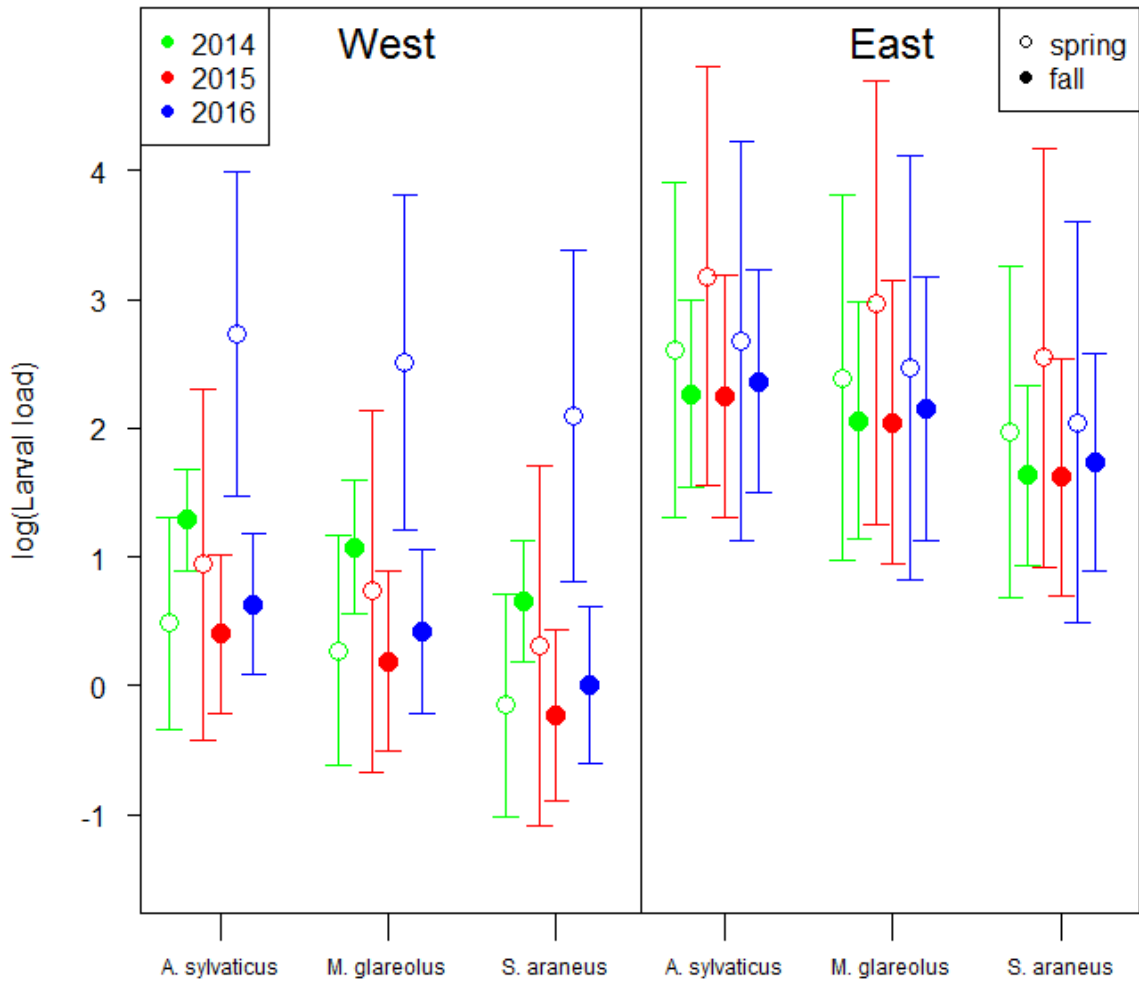
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623

624 Fig. 1

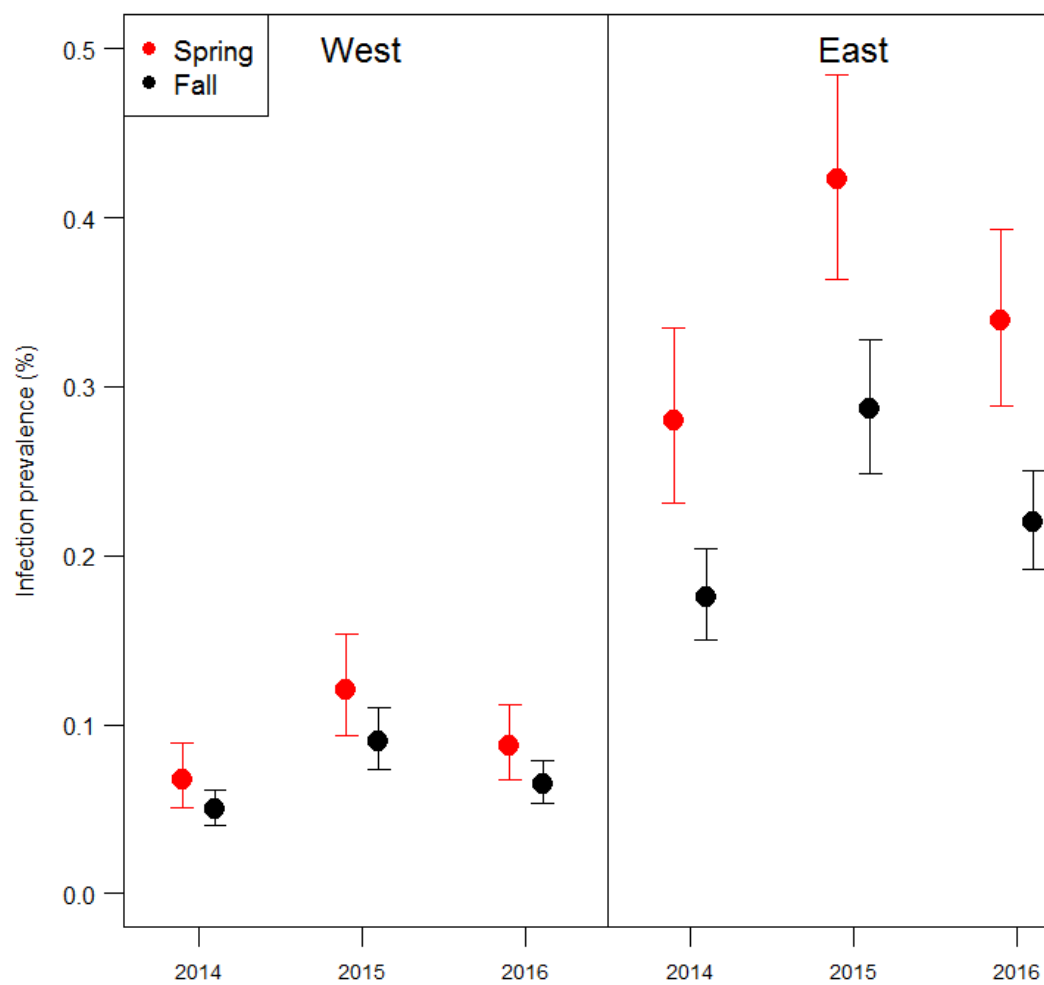




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626 Fig. 2

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628

629 Fig. 3

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