

12. The role of host diversity in *Borrelia burgdorferi* s.l. dynamics

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Abstract

There has been substantial debate about the influence of vertebrate host diversity on Lyme borreliosis risk. In North America, studies investigating *Borrelia burgdorferi* s.l. and the Black-legged tick (*Ixodes scapularis*) have shown that on a large spatial scale there seems to be a negative correlation between host species diversity and Lyme borreliosis risk. However, studies on this relationship in Europe are lacking. I discuss the work done in North America and translate the findings and assumptions of these studies to the European situation, where the sheep tick (*Ixodes ricinus*) is the most important vector of *B. burgdorferi* s.l. The European situation is fundamentally different compared to the North American situation due to the high diversity of *B. burgdorferi* s.l. genospecies, which are transmitted by different groups of vertebrate species. Disease risk in Europe is hypothesised to increase with vertebrate diversity due to an increase in *B. burgdorferi* s.l. genospecies diversity. However, it seems that the majority of genospecies in Europe is transmitted by two functional groups of host species, rodents and thrushes, which are present in most vertebrate assemblages. Therefore, it seems plausible that a *dilution effect* can also occur in Europe. This might result in high risk in urban areas where a few dominant species are very abundant, among which the most important reservoir hosts for *B. burgdorferi* s.l. in Europe.

Keywords: biodiversity, dilution effect, host behaviour, host density, *Ixodes ricinus*, *Ixodes scapularis*, urbanisation

Introduction

The presence and abundance of ticks is determined by the combination of a suitable microclimate and the presence and abundance of vertebrate host species, which is mainly present in forested areas (Randolph 2004). Tick-borne pathogens are transmitted to ticks by these host species and host species differ in their ability to transmit pathogens (Randolph 2009). Therefore, it seems logical that differences in tick-borne disease risk are related to differences in vertebrate assemblage composition. Vertebrates play an important role as (reservoir) hosts for both ticks from the *Ixodes ricinus* complex and *Borrelia burgdorferi* s.l. (Coipan and Sprong 2016, Földvári 2016, Heylen 2016, Hofmeester *et al.* 2016, Szekeres *et al.* 2016, Van Duijvendijk *et al.* 2016, Van Wieren and Hofmeester 2016). These host species differ in their quality as hosts for ticks and in their competence in transmitting *B. burgdorferi* s.l. Ticks can better feed from one host species than the other because of differences in grooming behaviour (Keesing *et al.* 2009) and immunological responses of hosts to feeding ticks (Dizij and Kurtenbach 1995). At the same time, some host species are better at transmitting *B. burgdorferi* s.l. to feeding ticks (i.e. have a higher reservoir competence) than other species (Kurtenbach *et al.* 1994), which differs for the different *B. burgdorferi* s.l. genospecies (Kurtenbach *et al.* 1998). Therefore, changes in host composition can change the number of ticks in the environment, the number of ticks infected with *B. burgdorferi* s.l. and the number of genospecies found in any tick population (Hofmeester *et al.* 2016).

In order to better understand the relationship between vertebrate host composition and Lyme borreliosis risk, I will try to answer the following three questions: (1) Which vertebrate species are

the best hosts for the most important vectors of *B. burgdorferi* s.l. in North America and Europe?; (2) Which vertebrate species have the highest reservoir competence for *B. burgdorferi* s.l.?; and (3) How are these species represented in different vertebrate assemblages? To answer these questions, I will first discuss the initial work on the relationship between host composition and Lyme borreliosis risk performed in North America, as most work on this subject has been done there. Afterwards, I will translate the North American findings to the European situation and relate this to the work that has been done in Europe. In the final section I will speculate about future changes in vertebrate distribution and abundance in Europe and the possible effects on Lyme borreliosis risk.

It all started in North America

Lyme borreliosis was first described in North America, where it was soon discovered that the disease was caused by a spirochaete transmitted by *Ixodes* spp. ticks (Burgdorfer *et al.* 1982). The most important vector in North America, the black-legged tick (*Ixodes scapularis*), was found to mainly parasitise white-footed mice (*Peromyscus leucopus*) as larva (Piesman and Spielman 1979) and white-tailed deer (*Odocoileus virginianus*) as adult (Watson and Anderson 1976). Humans are mainly bitten and infected by nymphal black-legged ticks, and therefore, the density of nymphs infected with *B. burgdorferi* s.l. was proposed as an important measure determining disease risk (Falco and Fish 1989). As a consequence, the white-footed mouse was pinpointed as the most important host determining disease risk for Lyme borreliosis, as the majority of infected nymphs had probably fed from this species (Mather *et al.* 1989).

A theoretical study showed that although deer are important hosts maintaining black-legged tick populations, it is mainly the density of hosts for immature ticks that determines the density of nymphs, *B. burgdorferi* s.l. nymphal infection prevalence (NIP) and eventually the density of infected nymphs (DIN; Van Buskirk and Ostfeld 1995). This is because, as soon as hosts for adult ticks are present, the number of hosts for the immature stages become limiting. Furthermore, Van Buskirk and Ostfeld (1995) showed that NIP was dependent on the ratio of species with high reservoir competence and species with low reservoir competence, while DIN was mainly influenced by the density of highly competent reservoir hosts. As a consequence of this model, most work on the influence of vertebrate hosts on NIP and DIN for *B. burgdorferi* s.l. has focused on hosts for immature black-legged ticks and their reservoir competence, especially because white-tailed deer (as hosts for adult black-legged ticks) are present in most forests (Augustine and Jordan 1998).

Based on the high reservoir competence for larvae of white-footed mice compared to other host species (Mather *et al.* 1989), and the fact that white-footed mice are omnipresent, Ostfeld and Keesing (2000a) proposed the dilution effect hypothesis. The dilution effect hypothesis states that disease risk increases with loss of biodiversity and was based on the ecology of Lyme borreliosis in North America (Ostfeld and Keesing 2000a). This hypothesis is based on the assumptions that: (1) white-footed mice are present in all vertebrate assemblages; (2) white-footed mice are the species with the highest reservoir competence; and (3) the distribution of ticks over the different host species is dependent on the relative abundance of these host species. In a species-poor assemblage, the relative proportion of white-footed mice was hypothesised to be highest resulting in a high proportion of the larvae feeding on this host species, and a high NIP and DIN. In contrast, in a species-rich assemblage, the relative proportion of white-footed mice was hypothesised to be lower, resulting in a lower proportion of the larvae feeding on this host species, and a lower NIP and DIN. A large scale study showed that Lyme borreliosis incidence was highest in states

with a low diversity of mammals and reptiles, but a high diversity of birds (Ostfeld and Keesing 2000a). Another early field test of this hypothesis showed that NIP was lower than expected if all larvae would feed on white-footed mice and the eastern chipmunk (*Tamias striatus*), the two species with the highest reservoir competence (Schmidt and Ostfeld 2001). Schmidt and Ostfeld (2001) calculated that as many as 60% of the larvae had to feed on other host species to obtain the observed NIP, showing that indeed the presence of other host species could reduce tick-borne disease risk. Furthermore, the results of Schmidt and Ostfeld (2001) suggest that although white-footed mice and eastern chipmunks feed an important proportion of black-legged tick larvae (~40%), a substantial amount of larvae take their blood meal from other host species.

Subsequent studies have shown that white-footed mice are indeed the species with the highest reservoir competence in North America (LoGiudice *et al.* 2003), and they were present in all fragments in a multi-state study investigating the relationship between host species diversity and Lyme borreliosis risk (LoGiudice *et al.* 2008). Furthermore, white-footed mice were found to be the least effective groomers (Keesing *et al.* 2009). Therefore, white-footed mice indeed seem to be the most ubiquitous species, which are the best host for both black-legged ticks and at the same time have the highest reservoir competence for *B. burgdorferi* s.l. However, using genetic techniques, Brisson *et al.* (2008) showed that only ~25% of black-legged nymphs infected with *B. burgdorferi* sensu stricto (s.s.) got their infection from white-footed mice, and that the more difficult to study shrews, masked shrew (*Sorex cinereus*) and short-tailed shrew (*Blarina brevicauda*) actually infected ~50% of the infected nymphs. Also, they estimated that ~50% of larvae get their blood meal from host species with a low reservoir competence (Brisson *et al.* 2008). This shows that multiple species of small mammal are important reservoir-competent hosts for *B. burgdorferi* s.s. in North America, and that other host species can indeed 'dilute' the infection prevalence in questing black-legged ticks. However, it was still the question if adding or losing host species would really change the distribution of ticks over the different host species, or if it would only mean that a different number of ticks would find a host.

Keesing *et al.* (2009) presented a model in which they included feeding success of larval black-legged ticks on six vertebrate host species in North America. They started with six host species and subtracted the species according to empirical data on host species presence in fragmented landscapes. The most reservoir competent species, the white-footed mouse and the eastern chipmunk were the last species to be left in the community, as these were generally present even in the most fragmented landscapes (LoGiudice *et al.* 2008). The modelling results showed that when subtracting less reservoir competent species, only 10% of larvae needed to be redistributed to the other host species for the DIN to increase. This showed that, in theory, only a fraction of the ticks that would otherwise feed on the added species need to be redistributed in order for a dilution effect to occur. In a recent study, Levi *et al.* (2016) tried to find empirical evidence for the percentage of ticks that redistribute over other hosts by looking at natural variations in white-footed mouse densities and testing for a correlation between mouse densities and the number of black-legged ticks feeding on white-footed mice. They found that both larval and nymphal burden decreased with rodent density and interpreted this as a redistribution of the same number of ticks over more host individuals with increasing density (Levi *et al.* 2016). However, the same correlation could be caused by changes in behaviour of white-footed mice with increasing density (Hofmeester 2016). These results show that there seems to be a mechanism reducing the encounter rate between white-footed mice and larval and nymphal black-legged ticks which is related to the presence and abundance of different vertebrate species in an assemblage. However, it is still unsure if this is caused by other hosts 'catching away' ticks from the most reservoir competent host species, or if this is caused by competition or predation-induced changes in host behaviour.

Although the generality of the dilution effect hypothesis has been questioned within the framework of Lyme borreliosis (Randolph and Dobson 2012, Wood and Lafferty 2013), recent work in North America showed that the risk of obtaining Lyme borreliosis is correlated with biodiversity. Turney *et al.* (2014) showed that in the USA, the incidence of Lyme borreliosis was negatively correlated with mammal host species richness and that this correlation was stronger in the most recent time period. I used the same data sources as Turney *et al.* (2014) to recreate their analysis with the most up to date data. Lyme borreliosis incidence in 2014 in 35 states in the western USA was negatively correlated with mammal host species richness (generalised linear model with negative binomial distribution and log link: $\beta = -0.24$, $P = 0.004$; Figure 1).

Lyme borreliosis is spreading towards the north in North America, and a study in Canada showed that there was a positive correlation between *Peromyscus* spp. density and the number of nymphal black-legged ticks infected with *B. burgdorferi* s.l., while the number of infected nymphs was negatively correlated to small mammal species richness (Werden *et al.* 2014). However, there is not always a negative correlation between species richness and DIN. In a study comparing species-poor islands with more species-rich mainland sites, there was no difference in NIP, while DIN was higher in the mainland sites (States *et al.* 2014). These results show that it is very difficult to infer mechanisms from large-scale studies. For example, it might be that there are more people recreating in areas with low mammal species richness, leading to an increase in Lyme borreliosis incidence. Furthermore, the identity of the species added or subtracted from a community is very important (Randolph and Dobson 2012), which was acknowledged as one of the assumptions for a dilution effect to occur (Ostfeld and Keesing 2000b). Therefore, it is important to study the presence/absence and densities of specific host species at a small spatial scale to better understand the mechanisms behind a possible *dilution effect* at a larger spatial scale.

Several small mammals (eastern chipmunk, masked shrew, short-tailed shrew, and white-footed mouse,) are clearly the most important host species feeding larval black-legged ticks and infecting these ticks with *B. burgdorferi* s.l. (Brisson *et al.* 2008, Levi *et al.* 2016). It is also clear that these

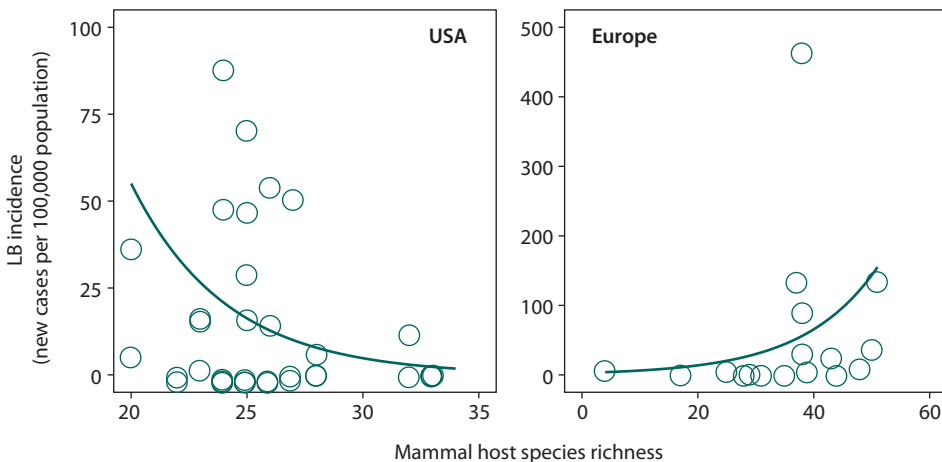


Figure 1. Correlation between Lyme borreliosis (LB) incidence and the species richness of mammal hosts in (A) North America and (B) Europe. Solid lines represent the outcomes of two generalised linear models.

species are present everywhere, even in the most fragmented landscapes, and therefore, it seems self-evident that the risk of getting Lyme borreliosis in North America is indeed related to the number of larvae feeding on small mammals. There is, however, mixed evidence for a dilution effect of host species diversity both on a large and small spatial scale. The big question that still remains is: Can all the work done on biodiversity, different vertebrate hosts, black-legged ticks and *B. burgdorferi* s.l. be translated to the European situation?

Translation to Europe

There are two important differences between North America and Europe with respect to ticks and *B. burgdorferi* s.l. First, in Europe, the most important vector for *B. burgdorferi* s.l. is another tick species, namely the sheep tick (*I. ricinus*). However, this should not make a very big difference as the sheep tick is closely related to the black-legged tick (Xu *et al.* 2003) and both species have a similar ecology (Gray 1998). Secondly, in Europe, a distinction is made between the different genospecies of *B. burgdorferi* s.l., which are transmitted by different groups of host species (Kurtenbach *et al.* 2002). Therefore, the correlation between mammal species richness and Lyme borreliosis risk (Ostfeld and Keesing 2000a, Turney *et al.* 2014, Werden *et al.* 2014) and all findings related to the mechanisms behind this correlation in the North American system (e.g. Keesing *et al.* 2009, Levi *et al.* 2016, LoGiudice *et al.* 2008) cannot be directly translated to the European situation. I will try to pinpoint the important differences and possible similarities between the two systems and the implications for a possible dilution effect and the role of vertebrate hosts in determining *B. burgdorferi* s.l. infection risk for humans in Europe.

The ecology of the sheep tick is very similar to that of the black-legged tick (Gray 1998). Small mammals such as the wood mouse (*Apodemus sylvaticus*), yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Myodes glareolus*) seem to be the most important host species feeding the larval stage and deer such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) seem to be the most important host species feeding the adult stage (Coipan and Sprong 2016, Földvári 2016, Heylen 2016, Hofmeester *et al.* 2016, Szekeres *et al.* 2016, Van Duijvendijk *et al.* 2016, Van Wieren and Hofmeester 2016). Therefore, host species richness might not be well correlated to densities of hosts for the two stages, as a system with roe deer and wood mice might function similarly to a system with three rodent species and two deer species. The most important difference between North America and Europe in terms of hosts for ticks is, that in Europe, the majority of sheep tick nymphs seem to feed on birds (Földvári 2016, Heylen 2016, Hofmeester *et al.* 2016) making birds more important as hosts for ticks in the European compared to the North American situation.

Another major difference between most studies in North America and the European situation is that in Europe differences in ecology between the genospecies of *B. burgdorferi* s.l. have been acknowledged for some time (Kurtenbach *et al.* 1998), while most studies in North America do not distinguish between genospecies (e.g. LoGiudice *et al.* 2003, Werden *et al.* 2014). It might be that the differentiation between genospecies is not necessary in the north-eastern part of North America as the most abundant genospecies in questing black-legged ticks is *B. burgdorferi* s.s. (Margos *et al.* 2012). In Europe, several genospecies have been found in questing sheep ticks, which are associated with different host groups: *Borrelia afzelii* and *Borrelia bavariensis* are associated with rodents, *Borrelia spielmanii* with dormice and hedgehogs, *Borrelia lusitaniae* with lizards and *Borrelia garinii* and *Borrelia valaisiana* with birds (Margos *et al.* 2012). Due to this host differentiation of *B. burgdorferi* s.l. in Europe, NIP and DIN of *B. burgdorferi* s.l. might not be the best measure for Lyme borreliosis risk as different genospecies have different clinical manifestations

(Coipan and Sprong 2016, Coipan *et al.* 2016). Therefore, it might be better to look at the NIP and DIN for each genospecies separately, and it has been suggested that disease risk might increase with host diversity, as more host species might result in a higher genospecies richness (Ruyts *et al.* 2016).

The most prevalent *B. burgdorferi* s.l. genospecies in Europe are *B. afzelii*, *B. garinii* and *B. burgdorferi* s.s. (Rauter and Hartung 2005). These genospecies are transmitted by rodents and birds, making the presence and abundance of these species groups the most important determinants of Lyme borreliosis risk (Hofmeester *et al.* 2016). Furthermore, the two genospecies, *B. garinii* and *B. bavariensis*, that cause neuroborreliosis, the most severe clinical manifestation of Lyme borreliosis, are transmitted by birds and rodents (Coipan *et al.* 2016, Margos *et al.* 2012). In order for a dilution effect to occur, a distinction could be made between rodent-transmitted *Borrelia* spp. and bird-transmitted *Borrelia* spp., and in both cases the assumptions made by Ostfeld and Keesing (2000b) should be met: (1) there is variation in reservoir competence between host species; (2) the most reservoir competent host species are present in vertebrate assemblages with a low host diversity; and (3) ticks feed on hosts relative to the density of the different host species (Figure 2).

For rodent-transmitted *Borrelia* spp. the first two assumptions are met because there are differences between host species in reservoir competence and the species with the highest reservoir competence are all small rodents present in many forests in Europe (Hofmeester *et al.* 2016). Therefore it is important to know if the number of ticks feeding on each rodent is related to host diversity. As far as I know, there has only been one study on the correlation between host diversity and the number of ticks feeding on rodents in Europe. Krasnov *et al.* (2007) showed that the number of immature sheep ticks feeding on rodents was negatively correlated with rodent species richness. However, rodent species richness was highly correlated with rodent density, making it

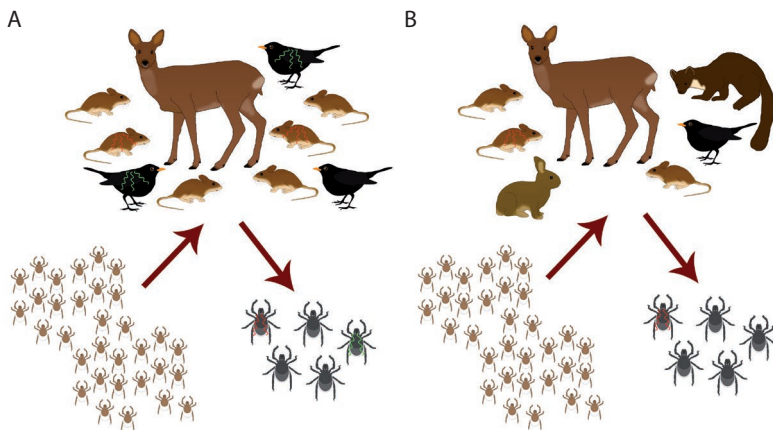


Figure 2. Schematic representation of the dilution effect hypothesis for vertebrate assemblages and the sheep tick in Europe. (A) A vertebrate assemblage with low species richness in which both black birds and wood mice are present in high density, resulting in a high density of infected nymphs with both rodent-transmitted *Borrelia* spp. (red spirochaetes) and bird-transmitted *Borrelia* spp. (green spirochaetes). (B) A vertebrate assemblage with higher species richness in which predators and competitors reduce densities of blackbirds and wood mice, and the relative number of larvae that will feed on these host species, resulting in a lower infection prevalence and a lower density of infected nymphs.

impossible to distinguish between the two parameters. Other studies have also shown that the number of larvae feeding on rodents decreases with rodent density (Hofmeester 2016, Kiffner *et al.* 2011). Furthermore, a recent study showed that tick burden on rodents decreased with the activity level of predators, such as the European pine marten (*Martes martes*), polecat (*Mustela putorius*), and red fox (*Vulpes vulpes*; Figure 3), in a plot resulting in a reduced DIN for rodent-transmitted tick-borne pathogens (Hofmeester 2016). Hofmeester (2016) suggested that this correlation could be caused by predator-induced changes in rodent behaviour. This mechanism might also explain the negative correlation found between red fox densities and Lyme borreliosis incidence in North America (Levi *et al.* 2012). This implies that if predator activity or density is correlated with host diversity, a *dilution effect* for rodent-transmitted *Borrelia* spp. is plausible.

For bird-transmitted *Borrelia* spp. there is also a substantial difference between birds in reservoir competence where thrushes of the genus *Turdus* have the highest reservoir competence (Hofmeester *et al.* 2016). The species with the highest reservoir competence, the blackbird (*T. merula*), is a very common species in many European countries and is present in most forested areas (Gregory *et al.* 2007). Furthermore, blackbirds have adapted to live in fragmented areas close to humans, making them an important host species determining Lyme borreliosis disease risk (Gregoire *et al.* 2002). Again, it is the last assumption that has to be verified to suggest a dilution effect in Europe for bird-transmitted *Borrelia* spp. Bird species that forage on the ground generally have higher tick burdens than species that forage in the canopy (Marsot *et al.* 2012). Therefore, it can be expected that changes in the foraging behaviour of blackbirds might change the number of ticks feeding on blackbirds and therefore NIP and DIN for bird-transmitted *Borrelia* spp. However, to my knowledge the correlation between blackbird tick burdens and differences in host assemblage has not been investigated.

The previous examples show that although there has been little work done to test the dilution effect hypothesis in Europe, the possible mechanisms behind an expected dilution effect have partly been studied. These studies show a big similarity between the North American and the European situation in terms of mechanisms. It is the density and number of immature ticks feeding on reservoir-competent species compared to reservoir-incompetent species that determines NIP and DIN. To test if this similarity on a small spatial scale results in a similar pattern on a larger spatial scale, I performed an analysis similar to the one performed by Turney *et al.* (2014) but for the European situation. I used Lyme borreliosis incidence data as summarised and standardised



Figure 3. Predators such as (A) the European pine marten (*Martes martes*), (B) the polecat (*Mustela putorius*) and (C) the red fox (*Vulpes vulpes*) can reduce tick burdens on rodents (photos by Tim Hofmeester).

for Western European countries by Sykes and Makiello (in press) and correlated these with the number of mammalian host species for the sheep tick present in each country. I used the list of host species provided by Anderson and Magnarelli (1993) and the presence/absence of species as described in the database of the IUCN (2014) to determine the mammalian host species richness per country. In Europe, Lyme borreliosis incidence increased with mammal host species richness (generalised linear model with negative binomial distribution and log link: $\beta=0.08$, $P=0.02$; Figure 1). The positive correlation in Europe might be caused by the fact that many of the mammalian host species are mice, voles and shrews, all relatively good reservoirs for rodent-transmitted *Borrelia* spp. (Hofmeester *et al.* 2016). These species might be able to fulfil the same ecological role in different habitats or parts of a country causing a rescue effect, as was suggested by Ostfeld and Keesing (2000a). This contrasting result shows that, although mechanisms on a small scale might be very similar, factors influencing Lyme borreliosis incidence on a large scale might be very different between continents. This analysis also indicates that a correlation between mammal host species richness per state or country might not be a good predictor of Lyme borreliosis incidence and other factors such as recreation habits of people might be far more important (Vanwambeke *et al.* 2010).

The work in North America and Europe shows that, on a small spatial scale, it is the specific identity of host species that determines their role in tick-borne pathogen dynamics, and biodiversity is only related to tick-borne pathogen risk if there is a correlation between the presence and abundance of specific host species and biodiversity (Randolph and Dobson 2012). Multiple species are important for both black-legged ticks and sheep ticks as maintenance hosts, reservoir-competent hosts and reservoir-incompetent hosts. Therefore, the study of mechanisms related to specific host species rather than biodiversity is needed to better understand the drivers of acarological hazard in both North America and Europe. In Europe, the most important host species that can be distinguished are several species of deer (as hosts for the adult stage of the sheep tick), several species of small mammal (as hosts for the larval stage and reservoirs for rodent-transmitted *Borrelia* spp.), and several species of thrush (as hosts for the nymphal stage and reservoirs of bird-transmitted *Borrelia* spp.). Other species, such as competitors or predators might influence the density or tick burden of these species groups, changing tick-borne pathogen dynamics (Hofmeester 2016, Keesing *et al.* 2006).

Looking into the future

Sheep tick populations have expanded and increased in density over the last couple of decades (Medlock *et al.* 2013). This can be partly explained by an increase in distribution and abundance of several of the most important host species such as bank voles, blackbirds, red deer and roe deer (Apollonio *et al.* 2010, Gregory *et al.* 2007, Van Strien *et al.* 2015). These species have most probably been so successful because they have been able to adapt to a fragmented and human-dominated landscape (Hewison *et al.* 2001, Michel *et al.* 2006). In the future, vertebrate assemblages are expected to further change as both small to medium-sized (Proulx *et al.* 2005) and large (Chapron *et al.* 2014) carnivores have also started to increase their distribution in Europe.

The increase in carnivores and the return of apex predators to some parts of Europe (Chapron *et al.* 2014) might result in cascading effects on Lyme borreliosis risk by changes in prey behaviour. The three host groups most important for maintaining sheep tick populations, deer, thrushes and rodents, are all prey species. It is well known that prey species can change their behaviour as a response to predators. Rodents reduce their time spent active, moving less and changing their spatial behaviour (Borowski and Owadowska 2010, Haapakoski *et al.* 2015) and blackbirds

decrease the time spent on the ground as a response to predators (Post and Götmark 2006). Both of these changes in behaviour will lead to a decrease in encounter rate between hosts and immature ticks, leading to a decrease in NIP and DIN for *B. burgdorferi* s.l. (Hofmeester 2016). Also, deer can change their habitat use in relation to predation risk (Tufto *et al.* 1996) and predators might also impact deer population densities (Melis *et al.* 2009). Furthermore, intra-guild predation or competition between predator species will affect tick-borne pathogen dynamics, as was shown in North America, where Lyme borreliosis incidence decreased with red fox density, but increased with coyote (*Canis latrans*) density (Levi *et al.* 2012). Therefore, the current comeback of carnivores in Europe might have impacts on Lyme borreliosis risk in the future, but the exact outcome will be hard to predict.

Another change in distribution and behaviour of vertebrate hosts for ticks in Europe is the adaptation of species to living in urban areas. More and more bird species have adapted to living in an urbanised world (Møller 2008), and rodents have been thriving close to humans for centuries (Meyer 2003). Although deer might not be present in the centre of urbanised areas, roe deer have formed small populations in city parks (Wang and Schreiber 2001). In the current situation, tick populations in the city seem to be relatively low, and blackbirds living in urban areas have a lower tick burden than blackbirds living in the forest (Gregoire *et al.* 2002). However, with increasing deer densities in the city as a possible response on the comeback of apex predators, this might change. Furthermore, by moving into the city, ticks might come into contact with novel host species. For example, brown rats (*Rattus norvegicus*), that are absent in most forests, are an important host for ticks in urban environments (Matuschka *et al.* 1996). This spillover into new host species is very hard to predict and might result in novel host species with a very high reservoir competence (Morse *et al.* 2012).

Within cities, deer might be present in city parks, while hedgehogs might take over the role of deer as maintenance hosts in gardens (Pfäffle *et al.* 2013). The release from predation has been suggested as the driver of increased hedgehog abundances in urban areas (Hof *et al.* 2012, Poel *et al.* 2015). Both the European hedgehog (*Erinaceus europaeus*) in western Europe and the Northern white-breasted hedgehog (*Erinaceus roumanicus*) in eastern Europe have been suggested to be reservoirs for different genospecies of *B. burgdorferi* s.l. including one of the causative agents of neuroborreliosis, *B. bavariensis* (Coipan *et al.* 2016, Skuballa *et al.* 2012). Hedgehogs are infested with both the sheep tick and the more specialised hedgehog tick (*Ixodes hexagonus*), which can both transmit *B. burgdorferi* s.l. (Pfäffle *et al.* 2011, Skuballa *et al.* 2012). The hedgehog tick is a nest-dwelling tick, and is therefore less prone to desiccation compared to the sheep tick, which might result in higher numbers of hedgehog ticks on hedgehogs compared to sheep ticks in urban environments (Gern *et al.* 1997). This might result in the hedgehog tick playing an important role in *B. burgdorferi* s.l. maintenance in urban areas (Pfäffle *et al.* 2011). Therefore, this tick species should also be considered in studies investigating the role of different vertebrate species in determining Lyme borreliosis risk in urban environments.

The blackbird is an important host species for another neuroborreliosis causing genospecies, *B. garinii* (Coipan *et al.* 2016). Blackbirds are present in high densities in urban areas, especially in gardens (Luniak *et al.* 1990). Generally, the few species that survive in urban areas occur in high densities (McKinney 2006), which suggests that reservoir-competent species, such as blackbirds and hedgehogs, can reach high densities in urban areas. Due to these high densities, the infection prevalence in ticks in cities and city parks might be very high as was found in a city park in Munich (Fingerle *et al.* 2008). The large amount of time people spent in city parks and gardens further increases the risk of getting Lyme borreliosis in these habitats (Mulder *et al.* 2013, Rizzoli *et al.*

2014). As a result, tick-borne disease risk in urban areas might already be higher than expected, and will most probably increase in the near future. Therefore, studies in urban areas are needed to better understand how urbanisation, adaptation of vertebrate hosts and spillover into novel host species will influence Lyme borreliosis risk.

Conclusion

There is a negative correlation between mammal host species richness and Lyme borreliosis incidence in North America, while this correlation is positive in Europe. At the same time, studies investigating the mechanisms at a small spatial scale show a large similarity between the North American and European situation. Therefore, it is far more important to study interactions between important host species rather than correlations with species richness or other metrics for biodiversity without studying the underlying mechanisms. Both in North America and in Europe, small mammals are important hosts for larval ticks, while deer are the most important hosts for the adult stage. In Europe, birds and especially thrushes also play an important role in feeding nymphal sheep ticks and infecting them with different genospecies of *B. burgdorferi* s.l. The most important host species for the sheep tick have increased in distribution and abundance in recent decades and are present in many parts of Europe, also in fragmented landscapes close to humans. Furthermore, these host species are all prey for predators, which might result in differences in tick-borne disease dynamics with changes in predator abundance. Several carnivore species are also increasing their distribution and abundance in Europe, which might lead to changes in tick densities and Lyme borreliosis risk in the future. Many vertebrate species are adapting to an urban landscape, including some of the most important host species for *B. burgdorferi* s.l. genospecies (*B. garinii* and *B. bavariensis*) that cause severe disease in humans. Very little is known about the circulation of these genospecies in urban areas. Therefore, the ecology of tick-borne pathogens in urban environments should be better understood, making this an important topic for future research.

Public health relevance

- Correlations on a large spatial scale between mammal host species richness and Lyme borreliosis incidence are not informative for the underlying mechanisms.
- In Europe, few species are important for feeding ticks (bank vole, blackbird, red deer, roe deer, wood mouse and yellow-necked mouse) and infecting them with *B. burgdorferi* s.l. (thrushes and rodents).
- Deer, thrushes and rodents are omnipresent and reside in fragmented and urban landscapes, close to humans.
- Predators might change the density or tick burden of these important host groups, changing tick-borne disease dynamics.
- Gardens are an important habitat in which Lyme borreliosis risk might be larger than expected.

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