



## Original article

Evidence for an effect of landscape connectivity on *Borrelia burgdorferi* sensu stricto dispersion in a zone of range expansion

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## ARTICLE INFO

## Keywords:

*Borrelia burgdorferi*  
Connectivity  
Landscape  
Lyme disease

## ABSTRACT

In North America, different strains of the Lyme disease-causing bacterium *Borrelia burgdorferi* sensu stricto cluster into phylogenetic groups that are associated with different levels of pathogenicity and, for some, specific rodent reservoir hosts. Here we explore whether landscape connectivity, by impacting host dispersal, influences *B. burgdorferi* s.s. spread patterns. This question is central to modelling spatial patterns of the spread of Lyme disease risk in the zone of northward range-expansion of *B. burgdorferi* s.s. in southeastern Canada where the study was conducted. We used multi-locus sequence typing (MLST) to characterise *B. burgdorferi* s.s. in positive ticks collected at 13 sites in southern Quebec, Canada during the early stages of *B. burgdorferi* s.s. invasion. We used mixed effects logistic regression to investigate whether landscape connectivity (probability of connectivity; PC) affected the probability that samples collected at different sites were of the same strain (MLST sequence type: ST). PC was calculated from a habitat map based on high spatial resolution (15 m) Landsat 8 imagery to identify woodland habitat that are preferred by rodent hosts of *B. burgdorferi* s.s. There was a significant positive association between the likelihood that two samples were of the same ST and PC, when PC values were grouped into three categories of low, medium and high. When analysing data for individual STs, samples at different sites were significantly more likely to be the same when PC was higher for the rodent-associated ST1. These findings support the hypothesis that dispersion trajectories of *B. burgdorferi* s.s. in general, and some rodent-associated strains in particular, are at least partly determined by landscape connectivity. This may suggest that dispersion of *B. burgdorferi* s.s. is more common by terrestrial mammal hosts (which would likely disperse according to landscape connectivity) than by birds, the dispersal of which is likely less constrained by landscape. This study suggests that accounting for landscape connectivity may improve model-based predictions of spatial spread patterns of *B. burgdorferi* s.s. The findings are consistent with possible past dispersal patterns of *B. burgdorferi* s.s. as determined by phylogeographic studies.

## 1. Introduction

Climate change is likely to drive emergence and re-emergence of vector-borne diseases and zoonoses (Gubler et al., 2001). Public and animal health professionals are increasingly aiming to predict the patterns of emergence of these diseases, in order to assess risk and to

inform disease management strategies (Gould and Higgs, 2009). Model-based prediction relies on knowledge of the biotic and abiotic components of the environmental niche of the pathogens and vectors, but the actual process of spread is frequently assumed or highly simplified (Bueno-Marí and Jiménez-Peydró, 2013). This may be adequate for some risk assessment processes, but for the purposes of targeted

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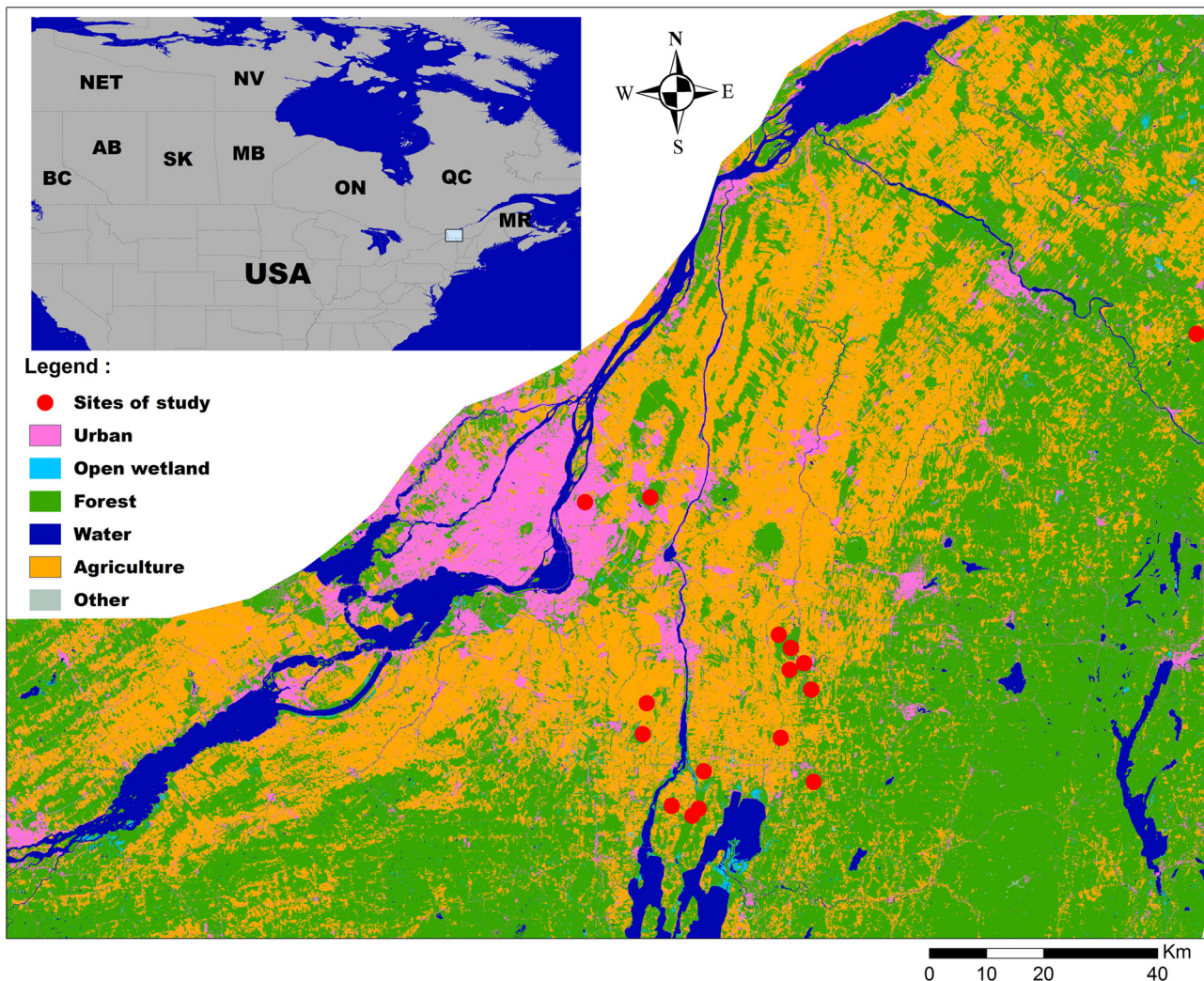
<https://doi.org/10.1016/j.ttbdis.2018.07.001>

Received 1 May 2018; Received in revised form 22 June 2018; Accepted 1 July 2018

Available online 02 July 2018

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**Fig. 1.** Study sites and landscape classification map. The sites where ticks were collected are shown by red dots on the landscape map of southern Quebec, Canada, obtained by classifying habitat according to Landsat 8 images. Some sites that are very close are represented by one dot (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

surveillance, prevention and control at a local level, the mechanisms (and thus trajectories) of pathogen invasion may be crucial. Lyme disease, caused by *Borrelia burgdorferi* sensu stricto (henceforth termed *B. burgdorferi* s.s.), is a vector-borne zoonosis that is emerging in North America and causing high public health impact. *Borrelia burgdorferi* s.s. is transmitted amongst wild animal reservoir hosts, particularly birds and rodents, by the tick *Ixodes scapularis* in the upper Midwestern and northeastern USA, and southcentral and southeastern Canada (Bouchard et al., 2015). The risk of Lyme disease due to *B. burgdorferi* s.s. has most recently emerged (and continues to emerge) in Canada due to northward spread of *I. scapularis* and *B. burgdorferi* s.s., and their hosts, associated with a warming climate (Leighton et al., 2012; Ogden et al., 2014; Simon et al., 2014). There is a critical public health need to identify other regions likely to be at risk (Ogden et al., 2014). *Borrelia burgdorferi* s.s. and immature *I. scapularis* are broadly host generalists, their hosts are woodland rodents and birds. Woodlands also provide refuges for ticks to survive over winter, and habitat for deer which are the main hosts for adult *I. scapularis* (Ogden et al., 2013a, 2013b). *Borrelia burgdorferi* s.s. is a diverse species with, at the time of writing, 138 strains identified to date in North America using multi locus sequence typing (MLST) (Margos et al., 2008; Mechai et al., 2016). Recently, we found evidence for associations of different strains of *B. burgdorferi* s.s. with different rodent host species (Mechai et al., 2016). These associations do not amount to complete host specialization;

rather they indicate that some strains are more efficiently transmitted by particular hosts, while the species remains a generalist (Mechai et al., 2016). Nevertheless, there is evidence that such host association may have shaped the phylogenetic tree of *B. burgdorferi* s.s., with major clades possibly having been associated with expansions of different host species with past, glacial-interglacial climate changes (Mechai et al., 2016; Ogden et al., 2015). The evolutionary ecology of *B. burgdorferi* s.s. has public health importance as different strains have different pathogenicity in humans (Hanincova et al., 2013), a phenotypic trait that may also have its origins in host associations (Mechai et al., 2016).

To understand and predict the occurrence of *B. burgdorferi* s.s. and its different strains, particularly in zones of invasion such as southern Canada, we need to understand how it is dispersed. Ticks have very limited capacity for dispersal by themselves (their lateral movements being limited to a meter at best (Stafford, 1992), so the bacterium can be spread by either feeding ticks carried by hosts or by infected hosts themselves. Consequently, host dispersal patterns will be key to *B. burgdorferi* s.s. dispersal. There is much evidence that passerine birds migrating north in spring and south in autumn facilitate long distance dispersal of ticks and *B. burgdorferi* s.s. This then provides a means to seed founder populations and drive range expansions (Humair, 2002; Ogden et al., 2008, 2013a, 2013b). Shorter scale dispersal by terrestrial mammals and non-migratory species may also play a role in dispersal at local spatial scales (Madhav et al., 2004). The relative contribution of

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