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Review

Ecology and Epidemiology of Lyme Disease in Western North America

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Simple Summary: Lyme disease affects about half a million Americans every year, and cases in Canada are rising. However, the number of studies focusing on the epidemiology of Lyme disease in western North America has been relatively low compared to that of eastern North America. Here, we aim to summarize the current state of knowledge regarding Lyme disease epidemiology in western North America, which includes current surveillance efforts tracking Lyme disease cases, modelling studies clarifying the geographic distributions of vectors for *Borrelia burgdorferi*, and the dynamics required to maintain and transmit *B. burgdorferi* in the natural environment. In providing a comprehensive picture of the state of Lyme disease in western North America, this review may be particularly helpful for future studies in the region.

Abstract: Lyme disease is the most common vector-borne disease in the United States and Canada. The causative agent of Lyme disease in North America is the spirochete *Borrelia burgdorferi*. In western North America, the primary vector of *Borrelia burgdorferi* is the western black-legged tick, *Ixodes pacificus*. Surveillance and modelling efforts indicate that *I. pacificus* is primarily found in coastal California, Oregon, Washington and the southern coastal regions of British Columbia However, infection rates with *B. burgdorferi* among *I. pacificus* ticks remain low, ranging from 0.6% to 9.9%. Lyme disease case numbers in western North America are also relatively low compared to eastern North America. Enzootic maintenance of *B. burgdorferi* by hosts in natural environments and climatic factors may influence Lyme disease risk. The borreliacidal western fence lizard, *Sceloporus occidentalis*, may contribute to the low infection rates observed in *I. pacificus* ticks, while the migratory nature of avian hosts can allow for long-distance tick dispersal. Moderately warm and moist environments and protection from sunlight define the suitable habitats of *I. pacificus* ticks. In this review, we discuss the ecology and epidemiology of Lyme disease in relation to *I. pacificus*, as well as the need for more studies in western North America.

Keywords: *Ixodes pacificus*; Lyme disease; habitat suitability modelling; *Borrelia burgdorferi*; western North America

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1. Introduction

Lyme disease is the most common vector-borne disease in the United States, Canada, and Europe [1–3]. Every year, nearly half a million Americans are treated and diagnosed with Lyme disease [3,4]. Reported cases in Canada increased from 144 in 2009 to 2634 in 2019 [5]. Lyme disease in humans is caused by bites of ticks infected with bacteria from the *Borrelia burgdorferi* sensu lato (s. l.) complex and is characterized by fever, headaches, fatigue, and a localized erythema migrans rash [6]. Despite being rarely lethal [7], Lyme disease can manifest into a disseminated illness that can lead to long-term complications associated with autoimmune responses, such as nerve and joint pain, facial palsy, and heart palpitations, if left untreated [6].

The spirochete *B. burgdorferi* Johnson et al. 1984 sensu stricto (s. s.), a member of the *B. burgdorferi* s. l. complex is the primary etiologic agent of Lyme disease in North America [8]. Certain tick species function as vectors that can transmit these spirochetes to humans.

In the eastern and mid-western United States and mid-southern and southeastern Canada, *Ixodes scapularis* Say is the primary vector of *B. burgdorferi* s.s. [9,10]. In western United States and southwestern Canada, *I. pacificus* Cooley and Kohls is the primary vector [9,10]. *Ixodes pacificus* has undergone several reclassifications, initially classified as *I. californicus* in 1908, revised to *I. ricinus* var *californicus* in 1911 [11–13], then determined as a distinct species in 1943 [11–13].

Ticks require blood meals in the larval and nymphal stages to molt to the next stage and in the adult stage to develop eggs. Each of the feeding life stages generally prefers a different set of vertebrate hosts (Figure 1). The life cycle of *I. pacificus* ticks, at least in California, takes three years (Figure 1), while the life cycle of *I. scapularis* usually takes 2 years in the United States [14] and 3–4 years in Canada [15].

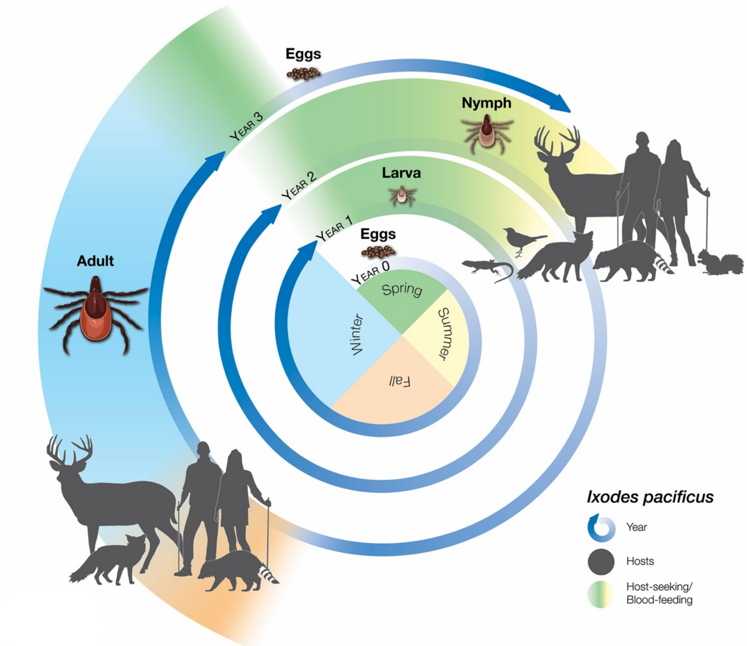

Figure 1. Life cycle of *I. pacificus* and the preferred hosts for each developmental life stage. Figure was retrieved from the United States Centers for Disease Control and Prevention [16].

Reported Lyme disease cases have steadily increased in the United States and Canada, but a majority of these cases are concentrated in the Northeast, mid-Atlantic, andupper Midwest of the United States [4,17,18] and Ontario, Quebec, and Nova Scotia in Canada [18]. In contrast, the western provinces of British Columbia, Alberta, and Saskatchewan have reported low numbers of Lyme disease and a higher proportion of travel-related cases acquired outside of the provinces [18].

The main goals of this review are to provide a brief overview of the ecology of *I. pacificus* and associated transmission dynamics of *B. burgdorferi* in western North America, to describe the environmental factors that influence the spread and distribution of *I. pacificus*, and to summarize previous efforts to predict the future distribution of *I. pacificus* and *B. burgdorferi* under different climate scenarios. Unless otherwise specified, subsequent mentions of *B. burgdorferi* refer to *B. burgdorferi* s.l.

2. Surveillance Efforts to Track Risk of Exposure to *Ixodes pacificus*

Tick surveillance is essential for assessing Lyme disease risk since ticks are the principal vectors for transmission. Tick surveillance methods can be either active, passive, or a combination of both. Active tick surveillance generally refers to the systematic collection of ticks either by use of carbon dioxide tick traps, direct removal from hosts captured from rodent traps, dragging a large, white cloth behind the investigator, or flagging, which involves waving a large, white cloth over vegetation ahead of the investigator [19].

Locations for active surveillance of ticks with relevance to Lyme disease are typically chosen based on the likelihood of human-tick contact, suitable habitats for ticks, and pre-existing surveillance data. Passive tick surveillance involves the submission of ticks from humans and vertebrate hosts (pets, livestock) by veterinary or medical professionals or members of the public to researchers or government agencies for tick identification or pathogen detection [19]. While useful in estimating the geographic distribution of tick vectors for *B. burgdorferi*, tick presence data does not indicate the importance of any given tick species in the transmission of Lyme disease. In addition to tick presence data, tick abundance and efficiency in acquiring and transmitting *B. burgdorferi* should also be considered.

Active tick surveillance done by public health agencies from California [20], Oregon [21], Washington [22], and British Columbia [23,24] indicates that *I. pacificus* is the most important *Ixodes* species for the transmission of Lyme disease in the western United States and Canada. From these active surveillance efforts, the current geographic range of *I. pacificus* is located along most of California, western Oregon, and Washington [21,22,25–27], and the southern coastal areas of British Columbia [26,28,29]. *Ixodes pacificus* adults comprise a majority of ticks obtained from many widescale surveillance studies using passive surveillance for Lyme disease vectors, but *I. pacificus* immatures are commonly reported from active surveillance efforts by ecological studies confined to smaller study areas [30–34]. This may be in part due to the focus on rodent hosts in such ecological studies.

Passive tick surveillance indicates that *I. pacificus* ticks account for a majority of human-biting tick submissions in western North America [24,33–35]. Most *I. pacificus* submissions originate from western California, Oregon, Washington, and the southern coastal regions of British Columbia [36,37]. The majority of *I. pacificus* ticks submitted were found on humans [33,34,36], although there are many cases where ticks are found on domesticated animals [23,33]. Adults are more frequently submitted to passive surveillance programs than immatures, despite peak adult host-seeking activity being greater in the winter or early spring, a season when humans are less likely to participate in outdoor activities [33,34]. The smaller sizes of *I. pacificus* immatures compared to adults make it less likely for humans to detect and subsequently report them [38]. Additionally, ascending vegetation to seek hosts is commonly done by *I. pacificus* adults but not nymphs [39]. Humans participating in outdoor recreational activities are likely to contact vegetation and, in turn, expose themselves to questing ticks.

The seasonal abundance of *I. pacificus* varies in western North America. Based on active [27,40–51] and passive [22,33,34,52] surveillance efforts in Northern California, Oregon, and Washington, *I. pacificus* nymphs are most abundant during the spring and early summer, while *I. pacificus* adults are most abundant during winter to early spring. In Southern California, both adult and nymphal *I. pacificus* have a shorter period of abundance compared to those in Northern California [50]. In contrast, seasonal abundance data from British Columbia indicate a slightly extended period of abundance, with nymphal and adult *I. pacificus* being abundant from spring to late summer and winter to late spring, respectively [26,28]. More work is needed to determine why periods of abundance for *I. pacificus* vary within western North America.

3. Infection Prevalence of *Ixodes pacificus* with *Borrelia burgdorferi*

Despite being the primary vector of *B. burgdorferi* in western North America, relatively lower proportions of *I. pacificus* ticks are infected with *B. burgdorferi* compared to *I. scapularis* in eastern North America. A common measure of Lyme disease risk is tick infection prevalence, which is the proportion of infected ticks among those collected in a study. Both active and passive surveillance have observed low infection prevalence in *I. pacificus* adults, ranging from 0.6 to 7.3% [21,22,33,52–58]. Nymphal infection prevalence is similarly low, although slightly higher than in adults, ranging from 1.4 to 9.9% [31,33,40,53,55,56,58–61]. These rates are considerably lower when compared with the infection prevalence for *I. scapularis* nymphs and adults, which can be as high as 23% [62] and 47% [63], respectively.

Studies of infection prevalence for *B. burgdorferi* in *I. pacificus* ticks have been conducted mainly on the west coast of North America, but interior western states and provinces have observed exceedingly low rates of infection. In Alberta, there are no established populations of *I. pacificus*, and numbers of *I. pacificus* ticks collected from the field and public submissions are concurrently low, with none reporting to carry *B. burgdorferi* [64,65]. In Utah, *I. pacificus* was the most common *Ixodes* tick found during a state-wide field survey from 2011 to 2013, but all were adults, and none carried *B. burgdorferi* [66]. Hence, the low infection prevalence of *B. burgdorferi* among *I. pacificus* ticks suggest an overall low risk of Lyme disease infection for humans and pets in western North America.

While the overall infection prevalence of *B. burgdorferi* is quite low for *I. pacificus*, infection prevalence can vary greatly between sites sampled in a study, and that conclusions taken from one site may not necessarily apply to other sites at different spatial scales. In Washington State, for example, Clallam County has seen elevated rates of *B. burgdorferi* infection among *I. pacificus* ticks compared to other counties, likely due to the rarity of the only incompetent host for *B. burgdorferi*, the northern alligator lizard, *Elgaria coerulea* (Weigmann), in the sites sampled within the county [22]. The lower infection prevalence of ticks in other counties may be due to the presence of the northern alligator lizard, along with other zooprophylactic lizards present in Washington State, such as the southern alligator lizard, *E. multicarinata* (Blainville), and the western fence lizard, *Sceloporus occidentalis* Baird and Girard [22].

Additionally, any interpretations and conclusions regarding tick infection prevalence should not rely on tick infection prevalence alone. For instance, Alberta and Saskatchewan have a higher tick infection prevalence than British Columbia [67], but this does not necessarily mean that Lyme disease risk is higher in those provinces. Historically, Alberta and Saskatchewan have received considerably fewer *Ixodes* spp. Ticks and most *Ixodes* ticks submitted are *I. scapularis* ticks that might have originated outside the provinces [67]. Therefore, a complete picture of Lyme disease risk should also consider endemic tick species composition, tick abundance, tick host availability, and where the ticks submitted to passive surveillance programs originated.

4. Surveillance Efforts Tracking Lyme Disease Cases

The number of reported human Lyme disease cases in western states and provinces is considerably lower than in eastern North America [68,69], which is consistent with the low infection prevalence observed in western North America. Lyme disease case numbers and seropositivity for canines in the west are also lower than in the east [70,71]. The incidence rate, which measures the number of people afflicted with Lyme disease per 100,000 of the population, ranged from 0.1 to 0.9 for California, Oregon, and Washington in 2020, a stark contrast from rates in the northeastern United States, which reached as high as 83.5 in the same year [68]. A similar pattern between the west and east is observed in Canada, where incidence rates ranged from 0.1 to 0.3 for provinces such as British Columbia, Alberta, and Saskatchewan, while eastern provinces have observed incidence rates ranging from 3.8 to 85.6 [5]. The low incidence rates observed for the western United States and British Columbia are unsurprising given the low infection prevalence with *B. burgdorferi* for *I. pacificus*. In California, peaks of Lyme disease cases in humans typically occur from May to July, indicating that transmission risk comes primarily from nymphal ticks, which are most active from April to June [72]. Lyme disease reports have also illuminated some behavioral factors and characteristics in humans that might account for increased exposure to *I. pacificus* and, in turn, Lyme disease. Generally, tick exposure and Lyme disease cases are associated with greater time spent outdoors in natural areas and pet ownership [34,52,73].

5. Mammalian and Reptilian Hosts and Their Roles in Lyme Disease Maintenance and Transmission

Lyme disease risk to humans does not only depend on the chances of encountering infected *I. pacificus* ticks but also on the effectiveness in which the Lyme disease spirochete itself is maintained and transmitted in nature. *I. pacificus* ticks must obtain the bacterial pathogen from feeding on infected hosts in their local environment. *I. pacificus* ticks can feed on a wide variety of animals, a characteristic that is paramount to the species' survival during each developmental life stage. Each life stage prefers different sets of hosts. Immature life stages of *I. pacificus* heavily prefer the western fence lizard, the southern alligator lizard, and the northern alligator lizard [26,28,29,47,59,74–77]. *I. pacificus* larvae and nymphs are also the predominant life stages found in avian hosts [48,76,78]. Small rodents such as the deer mouse, *Peromyscus maniculatus* (Wagner), the Pinyon mouse, *P. truei* (Shufeldt), the brush mouse, *P. boylii* (Baird), and the dusky-footed woodrat, *Neotoma fuscipes* Baird are also hosts that are heavily preferred by *I. pacificus* larvae [28,79]. *I. pacificus* adults seem to prefer larger mammals such as the black-tailed deer, *Odocoileus hemionus columbianus* (Richardson) [80].

Hosts that harbor heavy loads of *B. burgdorferi* can serve as a source of infection for feeding *I. pacificus* ticks and are termed reservoir hosts, while organisms that cannot carry the pathogen are considered incompetent. Furthermore, the importance of a host's role in the maintenance of *B. burgdorferi* in the environment is determined by their ability to successfully carry and spread the pathogen to feeding ticks. Table 1 provides a list of a few hosts that may play key roles in the maintenance of *B. burgdorferi* in western North America based on previously published studies.

Table 1. Key and potential hosts of *I. pacificus* and their efficiency as reservoirs for *B. burgdorferi*.

Host	Predominant Feeding *Ixodes pacificus* Life Stage	*I. pacificus* Infestation Levels	*B. burgdorferi* s.s. Infection Rates (Host)	*B. burgdorferi* s.s. Infection Rates (Attaching Ticks)	Studies
Peromyscus maniculatus	Nymphs	Low	Low	Low	[81–86]
Neotoma fuscipes	Larva	Moderate	Low	Low	[55,79,84,87–91]
Neotamias ochrogenys	Larva	Moderate	N/A	N/A	[92]
Sciurus griseus	Larva and nymphs	Moderate	High	High	[60,84,85,93–95]
Sceloporus occidentalis	Larva and nymphs	High	Low	Low	[47,74–77,96,97]
Elgaria multicarinata	Larva and nymphs	High	Low	Low	[59]
Junco hyemalis	Larva and nymphs	High	Low	Low	[48,58,76,78,79]
Pipilo maculatus	Larva	High	N/a	Low	[48,58,76,78,79]
Catharus guttatus	Larva	High	Low	N/A	[48,58,76,79]
Thryomanes bewickii	Larva	High	Low	Low	[58,76,78]
Certhia americana	Nymphs	Low	N/A	N/A	[48,78,79]
Haemorhous purpureus	Larva and nymphs	Moderate	N/A	N/A	[48,78,79]

Table 1 is not an exhaustive list of hosts, but it indicates key components that can explain both the maintenance of the Lyme disease spirochete in local environments and the lower numbers of Lyme disease cases in western North America compared to the east. Host characteristics relevant to the transmission of the Lyme disease spirochete, such as tick infestations, host infection prevalence, and tick infection prevalence, have been laid out in the table above. The effects of such characteristics on the prevalence of Lyme disease may be best explained through two key actors in the enzootic maintenance and transmission of Lyme disease spirochete: the western fence lizard and the western gray squirrel, *Sciurus griseus* Ord.

Ixodes pacificus larvae and nymphs prefer to feed on the western fence lizard rather than rodents, but this reptile species is an incompetent host for *B. burgdorferi* s.s. [47,74–77,96]. Spirochetal infection rates among ticks that have fed on these lizards are extremely low and attempts to isolate the Lyme disease spirochete have been unsuccessful [47,74,97]. Laboratory studies are underway to determine why western fence lizards are incompetent for the Lyme disease spirochete, but it has been suggested that the blood in this lizard species has a borreliacidal factor that destroys spirochetes present in *I. pacificus* ticks [98]. In habitats where western fence lizards are abundant, *B. burgdorferi* s.s. loads in *I. pacificus* immatures may be heavily diminished [60], which could naturally lead to a lower chance of humans acquiring Lyme disease from biting *I. pacificus* ticks. However, it is still unclear how the western fence lizard's refractory nature can affect *B. burgdorferi* infection [60,88]; hence more work needs to be done before concluding that this lizard species decreases *B. burgdorferi* s.s. loads in nature and, in turn, Lyme disease cases in nearby localities.

Conversely, the western gray squirrel seems to be a primary player in the enzootic maintenance and transmission of *B. burgdorferi* s.s. A high proportion of this species has already been reported to have long-lasting infections with *B. burgdorferi* s.s. it is in frequent contact with both *I. pacificus* larvae and nymphs and naturally acquired larval ticks that have fed on this species have been reported to carry *B. burgdorferi* s.s. [60,84,85,91,94,95]. In areas where the western fence lizard is rare or absent, the western gray squirrel may amplify *B. burgdorferi* s.s. in local enzootic cycles and subsequently increase Lyme disease risk.

In addition, these findings indicate that *I. pacificus* nymphs may play an important role in maintaining the enzootic cycle for *B. burgdorferi*. While *I. pacificus* nymphs highly prefer incompetent reptilian hosts, they are still capable of transmitting *B. burgdorferi* to a diverse array of mammalian and avian hosts (Table 1). In contrast, *I. pacificus* adults highly prefer deer, which are dead-end hosts for *B. burgdorferi*.

6. Avian Hosts and Their Role in Lyme Disease Transmission and Tick Dispersal

In North America, avian hosts may play only a small role in the maintenance of *B. burgdorferi* s.s. in local habitats compared to rodents and lizards, given the highly variable rates of infection among avian hosts [58,76,77] and the consistently low rates of infections among *I. pacificus* ticks, regardless of life stage [48,58,78,79]. However, the migratory nature of certain avian hosts, such as the Pacific wren, *Troglodytes pacificus* Baird, spotted towhee, *Pipilo maculatus* Swainson, Swainson's thrush, *Catharus ustulatus* (Nuttall), and fox sparrow, *Passerella iliaca* (Merrem) [99], could allow for long-distance tick dispersal and, in turn, the spread of *B. burgdorferi* s.s. to areas where Lyme disease is non-endemic [64]. Low numbers of *I. pacificus* immatures have already been found at coastal and inland sites of far-western Canada, likely due to migratory birds carrying *I. pacificus* ticks from the western United States [64]. Moreover, birds may also be able to disperse *B. burgdorferi* s.s. for long distances either by maintaining spirochetal infections for long periods of time or by reactivation of latent infection caused by migration stresses [58]. While avian hosts may be of little importance to the local maintenance and transmission of *B. burgdorferi*, they can have the capacity to introduce ticks infected with *B. burgdorferi* to areas where the Lyme disease pathogen is not yet established.

7. The Effects of Community-Level Dynamics on Lyme Disease Maintenance and Transmission

Being able to carry *B. burgdorferi* s.s. and efficiently transmit the pathogen to feeding ticks is important to the enzootic maintenance of *B. burgdorferi* s.s., but it is important to keep in mind that local community composition and ecological interactions can also influence the maintenance of *B. burgdorferi* and risk levels for Lyme disease in western North America [89]. For instance, while deer mice seem to act as dilution hosts reducing *B. burgdorferi* s.s. prevalence in a given habitat, it may be important in maintaining *B. burgdorferi* s.s. in other habitats where competition with more efficient hosts is absent [89]. Furthermore, increased predator diversity can reduce rodent movement and lead to less contact with tick vectors, which then reduces pathogen transmission in the environment and subsequently lowers Lyme disease risk [90].

Greater transmission of *B. burgdorferi* at a community level can also increase the chances of avian hosts acquiring infected *I. pacificus* ticks [100]. Rodent species richness, local mammal infection prevalence, and tick infection prevalence in a given site can be significant contributors to avian tick burden and infection prevalence [100].

Changes in the host composition of a given environment can also affect transmission dynamics. For instance, the western gray squirrel is a key player in the enzootic maintenance of B. burgdorferi s.s., yet its displacement by eastern gray squirrels, *S. carolinensis* Gmelin, and eastern fox squirrels, *S. niger* L., could dampen its contributions to overall Lyme disease risk in western North America [95,101]. Eastern gray squirrels and eastern fox squirrels have exhibited lower infection rates with *B. burgdorferi* s.s. [95]. Redwood chipmunks, *Neotamias ochrogenys* (Merriam), may also have some role in the enzootic maintenance of *B. burgdorferi* s.s. given that this species has been found with greater infestations of nymphal and larval *I. pacificus* compared to squirrels [102]. Interestingly, other chipmunk species in parts of the eastern United States and Europe contribute to *B. burgdorferi* s.l. transmission after introduction to the natural environment, hence future studies determining the effectiveness of redwood chipmunks as reservoir hosts for *B. burgdorferi* s.s. may be of some importance [103,104].

Thus, hosts contributing greatly to the maintenance of *B. burgdorferi* s.s. should be given great importance when determining possible areas of elevated Lyme disease risk, but the overall ecology and host composition of a given environment should also be considered when evaluating how efficiently *B. burgdorferi* s.s. is being maintained and transmitted in a given environment.

8. Additional Tick Vectors of the Lyme Disease Spirochete in Western North America

In addition to *I. pacificus*, other Ixodid ticks in western North America can also function as vectors for *B. burgdorferi* s.s. *Ixodes angustus* Neumann and *I. spinipalpis* Hadwen and Nuttall are competent vectors for *B. burgdorferi* s.s. [105,106], although these *Ixodes* species are more associated with other members of the B. *burgdorferi* s.l. complex than *B. burgdorferi* s.s. [86,107–109]. *Ixodes angustus* and *I. spinipalpis* may still participate in the enzootic transmission of *B. burgdorferi* in some capacity. *I. spinipalpis*, especially, is more successful in attaching and feeding to completion on certain rodents than *I. pacificus* [109] and has reported high infection rates of *B. burgdorferi* s.s. [110]. In the Pacific Northwest, *I. angustus* and *I. spinipalpis* ticks feeding on mammalian and avian hosts have been found in comparable numbers and infection rates to *I. pacificus* [107,111]. However, more laboratory studies are needed to determine the true efficiency of *I. spinipalpis* and *I. angustus* as vectors for *B. burgdorferi* s.s. In addition, both *I. spinipalpis* and *I. angustus* are occasional human biters; hence these tick species are of less importance regarding Lyme disease cases in humans [30].

Ixodes auritulus Neumann could also maintain and transmit *B. burgdorferi* s.s. in nature. Despite only feeding on avian hosts, *I. auritulus* may be relevant to the long-distance dispersal of the Lyme disease spirochete to nonendemic areas of Lyme disease, given the migratory nature of avian hosts and reports of *B. burgdorferi* s.s. infections among members of this species [64,99]. Migratory birds tend to be more infested with *I. auritulus* than *I. pacificus*, and based on the high infection prevalence observed among attached *I. auritulus* ticks, these migratory birds may have the capacity to act as reservoirs for *B. burgdorferi* s.s. [64,99]. Regardless of whether other *Ixodes* ticks play a larger role in the epidemiology of Lyme disease than *I. pacificus*, diverse tick communities may be favourable for the overall maintenance and circulation of the Lyme disease spirochete in local habitats. In southern California, infection of *B. burgdorferi* s.s. was predicted by diversity, specifically by *I. spinipalpis* and *I. peromysci* Augustson [112]. If *I. pacificus* populations are not frequently infected with *B. burgdorferi*, then the pathogen may be maintained in the landscape by other competent *Ixodes* species [112]. More robust maintenance systems might allow *I. pacificus* ticks to be more frequently infected with *B. burgdorferi* and, given their status as a bridging vector, increase the risk of Lyme disease to nearby human populations.

9. Environmental and Climatic Factors Affecting *Ixodes pacificus* and *Borrelia burgdorferi*

For *B. burgdorferi* to be successfully transmitted from the natural environment to humans, both a robust system of maintenance by hosts in the natural environment and efficient bridging vectors that have the tendency to bite humans are required. Besides the availability of hosts for *I.pacificus*, tick abundance, tick biting behaviors, and the presence of alternative tick vectors, the enzootic maintenance and transmission of *B. burgdorferi* can also be affected by climatic factors such as humidity and temperature. Most published studies in western North America have been done in California and focus on the effects of such climatic factors on the primary tick vector, *I. pacificus*, to gauge how the maintenance and transmission of *B. burgdorferi* will be affected by changes in the weather and climate.

In general, environments that are moderately warm and moist support greater numbers of *I. pacificus* ticks in the west [40,51,113]. Specifically, moderately warm temperatures can activate host-seeking activities and accelerate the development of all three life stages of *I. pacificus*, leading to an increase in overall numbers for the tick [51,114]. Greater humidity has also been shown to prolong the survival of larval and nymphal *I. pacificus* [50,115]. The greater numbers of *I. pacificus* ticks in moderately warm and moist environments typically coincide with a higher infection prevalence for *B. burgdorferi* [112,113,116]; hence Lyme disease risk may be greater in such areas.

A good example illustrating the effects of humidity and temperature on *I. pacificus* ticks and *B. burgdorferi* is the stark contrast between northern and southern California in terms of Lyme disease cases, tick abundance, and infection prevalence among ticks. Infection prevalence among ticks is greater in the environments of northern and coastal California than in the hotter and drier regions of southern California [53,54,117]. This corresponds with the lower Lyme disease cases observed in southern California than in northern California [43]. The relatively unfavourable environment in southern California may cause a truncation in the host-seeking period of *I. pacificus* ticks [50], which, in turn, could make it less likely for *I. pacificus* ticks to be infected with *B. burgdorferi* and subsequently cause Lyme disease infections in humans.

The effects of temperature and humidity on *I. pacificus* and *B. burgdorferi* transmission can also be seen in the different habitat types present in western North America. Overall tick burdens are generally higher in forested areas, such as dense oak woodlands and woodland-grass than in chaparral habitats, likely due to the former habitats having more surface ground cover and canopy cover, protecting desiccation-sensitive *I. pacificus* ticks from extremely high temperatures and lower humidity that are especially evident in warmer months [40,47,78]. Furthermore, *B. burgdorferi* infections among hosts are more frequently observed within woodland and woodland-grass habitats than chaparral or grassland habitats [85,108,116,118,119]. The former habitats may protect ticks from environmental extremes, encouraging host-seeking behaviors and perhaps a more effective system of maintaining *B. burgdorferi* in the environment.

Within woodland types, it is interesting to note the infection prevalence of *B. burgdorferi* among *I. pacificus* nymphs are slightly greater in hardwood-dominated woodlands, such as oak woodlands, that tend to be hotter and drier than conifer-dominated woodlands, such as redwood and pine woodlands [61,85,112,120,121]. This trend is seemingly the opposite of what has been observed in studies looking at broader spatial scales, further stressing the importance of the effect that specific sites can have on tick abundance and infection prevalence.

Coastal habitats may also provide a beneficial environment for host-seeking *I. pacificus* and *B. burgdorferi*, given the higher humidity and more stable temperatures in such habitats [86]. With these environmental conditions, coastal habitats tend to have greater tick burdens on hosts, a greater diversity of *Ixodes* ticks, and a greater prevalence of *B. burgdorferi* infection among ticks than hotter and drier areas [86], which could perhaps lead to greater Lyme disease risk. Coastal counties in California [122] and Oregon [21] have already reported the majority of locally acquired Lyme disease cases in their respective states. In British Columbia, the risk of Lyme disease is greatest in coastal areas as well [123].

Environmental conditions at a local scale can also have an indirect impact on Lyme disease risk via effects on existing tick and host populations. The presence of leaf litter and tree cover provides protection from sunlight and facilitates a cool and moist environment that is advantageous both to *I. pacificus* ticks and certain hosts [42,46,48,84,113,124]. For instance, bird species that frequently use leaf litter as substrates are more heavily infested by *I. pacificus* than bird species that rarely use or do not have access to such substrate [48,84]. Lizards carry heavier tick loads in woodlands than in open grassland and when leaf litter is present [75]. Moss on trees provides a similar effect as it reduces surface temperature and increases humidity on trees [118]. Models also indicate that nymphal densities are greater in areas with soils that have slow infiltration rates, which hold more moisture and provide favourable microclimatic conditions for nymphs [121].

Picnic areas and trails are areas where humans can encounter *I. pacificus* ticks during recreational activities. Wooden tables, benches, tree trunks, and logs in picnic areas are common sites for questing *I. pacificus* nymphs [31,40,46,118]. Questing nymphs more frequently occur in trunks and logs than leaf litter [31,40,118]. Resting against wooden materials also poses a greater risk of exposure to *I. pacificus* ticks than contacting leaf litter [31,46]. This apparent preference may be due to western fence lizards and western gray squirrels, both primary hosts of *I. pacificus*, displaying key behavioral activities on wooden materials, and these hosts may be depositing attractant chemicals on logs and trunks [40,118]. Also, *I. pacificus* adults occur more frequently on trails with adjacent vegetation than on sun-exposed trails and open, grassy hillsides [42,49,124]. However, the chances of encountering host-seeking *I. pacificus* ticks along trails are still low as visitors most often walk along the centre of such trails away from the vegetation present along trail borders [124]. While picnic areas and certain trails provide a low-to-moderate risk of acquiring host-seeking *I. pacificus* ticks, there is an even lower risk of acquiring Lyme disease when considering the low infection prevalence of *B. burgdorferi* among *I. pacificus* ticks [31,46,124,125].

10. Modelling the Geographic Distributions of *Ixodes pacificus* and *Borrelia burgdorferi*

Remote sensing, geographic information systems (GIS), and modelling approaches can be useful in delineating the interactions between wildlife, livestock, and humans in the context of disease transmission [126–130]. A common way to apply knowledge of competent tick vectors and reservoir hosts for *B. burgdorferi* to Lyme disease surveillance efforts is to develop species distribution models that determine the geographical distribution of the tick species and pathogen of interest. Species distribution models can evaluate the suitability of different environments for ticks and the pathogens they carry and aid in the creation of habitat suitability maps [131], which can be especially useful in informing public health surveillance programs and educating the public about high- and low-risk areas of exposure.

Known locations of *I. pacificus* ticks and *I. pacificus* ticks infected with *B. burgdorferi*, respectively, are needed to develop species distribution models that accurately predict suitable habitats of *I. pacificus* and *B. burgdorferi* [36,121–123,132–136]. Species distribution models also need to incorporate biotic and abiotic variables to accurately predict areas of suitable habitat since environmental factors can affect tick survival and, in turn, the survival of ticks carrying pathogens [120,121,123,133–138].

Model building can begin once all the necessary inputs have been collected. Notably, most modelling attempts in western North America focus only on the geographic distribution of *I. pacificus*. A variety of machine-learning techniques, programs, and algorithms have been used to map the geographic range of *I. pacificus* (Table 2). Given the different modelling methods available, it is important to be aware of the different biases and assumptions that each method has.

Results from modelling studies have illuminated the geographic ranges for *I. pacificus* and *B. burgdorferi* across western North America. In British Columbia, *I. pacificus* ticks were projected to have suitable habitats along the south, central, and north coast and in valley systems in the interior of the province [123], consistent with areas of known Lyme disease risk in the province [139]. In the western United States, the predicted habitat for *I. pacificus* is quite wide, concentrating on the coastal and northwest areas of California, western Oregon, and western Washington [136]. In California, particularly, suitable habitat for *I. pacificus* ticks focuses on areas with moderate amounts of cold-season precipitation and cold-season temperatures greater than 0C [134,140]. These areas include coastal regions in northwest California and along the Sierra Nevada foothills, which are also the same regions where Lyme disease cases are observed [122,134]. In Alaska, the current suitable habitat for *I. pacificus* ticks is in the southeast region of the state, in valleys around Anchorage, lowlands on the Kenai Peninsula, and the islands north of Kodiak [138].

Table 2. Species distribution modelling methods used to map the geographic distributions of *I. pacificus and B. burgdorferi* in western North America. Adapted from Pearson 2010 [141].

Species Distribution Modelling Method	References for Method	Species Dataset Required	Sample Studies
Maximum Entropy (MaxEnt)	Phillips, S.J., R.P. Anderson, and R.E. Schapire (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, pp. 231–259.	Presence	[111,112,122,131,133,134,137]
Boosted Regression Trees (BRTs)	Elith, J., C. Graham, and the NCEAS species distribution modeling group. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), pp. 129–151.	Presence or Presence/Pseudo-absence	[111,112,133,134,137]
Multivariate Adaptive Regression Splines (MARS)	Elith, J. and Leathwick, J.R. (2007). Predicting species' distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions*, 13, pp. 165–175. Leathwick, J.R., Elith, J., and Hastie, T. (2006). Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecological Modelling*, 199(2), pp. 188–196.	Presence/Absence or Pseudo-absence	[111,112,133,134,137]
Generalized Linear Models (GLMs)	Lehman, A., Overton, J.M., and Leathwick, J.R. (2002). GRASP: generalized regression analysis and spatial prediction. *Ecological Modelling*, 157, pp. 189–207.	Presence/Absence or Pseudo-absence	[111,112,133,134,137]
Genetic Algorithm for Rule-Set Prediction (GARP)	Stockwell, D.R.B., and D.P. Peters. 1999. The GARP modelling system: Problems and solutions to automated spatial prediction. *International Journal of Geographical Information Systems*, 13, pp. 143–158.	Presence	[109]
Random Forest (RF)	Breiman, L. (2001). Random forests. *Machine Learning*, 45, pp. 5–32.	Presence/Absence or Pseudo-absence	[111,112,133,134,137]

Only a few published studies from British Columbia have attempted to map the suitable habitats of *I. pacificus* ticks carrying *B. burgdorferi*, with said habitats concentrating along the Vancouver Island coast, southwest coast of the mainland, and in certain valley systems in interior British Columbia [123].

Climate projections and forecasted land use and ecoregions are typically needed to account for future environmental conditions [133] to project future geographic ranges of *I. pacificus* and *B. burgdorferi*. Normally, Global Circulation Models (GCMs) and Representative Concentration Pathways (RCPs) are used to determine future suitable habitats. GCMs are numerical models that represent the physical processes in the atmosphere, ocean, cryosphere, and land surface, and they are used to simulate the response of the global climate system to increasing greenhouse gas concentrations [142]. RCPs represent different projections for greenhouse gas concentrations extending up to 2100 [143]. Multiple GCMs and RCPs are used when considering the uncertainty in future bioclimatic predictions and variation in different climate change projections [133,138,140].

Future predictions have mostly focused on the suitable habitat of *I. pacificus* and are mostly made for California, where forecasts have been conflicting [136,140]. This discrepancy is likely due to a combination of factors, including the use of ensemble modelling versus a single modelling approach, differing tick presence points, data resolution, and geographical ranges used for the study area [133,140]. Variable predictions can be seen between different climate change scenarios as well. In general, more severe RCP scenarios project greater geographical distribution of *I. pacificus* compared to milder RCP scenarios [133,136,140]. The risk of human exposure to *I. pacificus* is expected to substantially increase regardless of any future scenario [133,138,140] due to the proximity and overlap of suitable habitats with developed and public land, respectively. So far, no study regarding future predictions for *I. pacificus* distribution has been conducted for Canada. There have also been no published studies on the future distribution of *I. pacificus* ticks and Lyme disease in western North America.

While the habitat suitability maps developed in recent years have been helpful in determining the current and future geographic distribution of *I. pacificus*, it is important to remember that most of these findings are based on tick surveillance data that does not discriminate between *I. pacificus* life stages. In addition, given the low rates of infection with *B. burgdorferi*, habitat suitability maps for *I. pacificus* should not be considered Lyme disease risk maps. The development of more *I. pacificus* distribution maps beyond California and *B. burgdorferi* distribution maps in western states and provinces is needed to provide a clearer picture of Lyme disease risk in western North America.

11. Conclusions

Despite the relatively low infection prevalence of *B. burgdorferi* among *I. pacificus* ticks, extensive work has been conducted to understand the ecology and epidemiology of Lyme disease in western North America. However, additional research on Lyme disease ecology in the region, particularly in areas where Lyme disease is an emerging risk, is needed to supplement the current literature that is focused primarily on California. It is quite possible that the differing abundances of available mammalian and avian hosts, alternative vector species, and the diverse environments present in western North America provide the opportunity for different tick-host-pathogen dynamics across the region. A more comprehensive view of *I. pacificus* ecology and Lyme disease epidemiology in the west requires intense research in the region that uses active surveillance methods, the creation of long-term tick collections, and increased collaboration between experts from various fields from public health and ecology to geography and climate science.

With issues regarding climate change and increasing CO_2 emissions, there is also more work to be done in determining current and future suitable habitats for both *I. pacificus* and *B. burgdorferi.* Much of the published research on this front has, again, focused only on California. Hence there is a strong need to develop habitat suitability maps along western North America. More intensive active surveillance efforts, along with the promotion of online platforms for tick reports, such as e-Tick in Canada [36] and TickReport in the United States [144], can provide a better picture of the geographic distribution of *I. pacificus* and aid in modelling efforts.

While habitat suitability maps for *I. pacificus* can be of great importance for public health education and surveillance, they should not be used as proxies for Lyme disease risk, as the infection prevalence of *B. burgdorferi* is still extremely low in *I. pacificus* compared to *I. scapularis*. Still, determining the geographic range of *I. pacificus* can be useful in deciding where public education initiatives and proper protective measures should be employed to mitigate Lyme disease risk. Furthermore, the creation of more habitat suitability maps for *I. pacificus* and risk maps for *B. burgdorferi* will be incredibly helpful in gauging Lyme disease risk at larger spatial scales and will contribute to current literature on the ecology and epidemiology of Lyme disease in western North America.

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