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The Impacts of Climate Change on Ticks and Tick-Borne Disease Risk

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Abstract

Ticks exist on all continents and carry more zoonotic pathogens than any other type of vector. Ticks spend most of their lives in the external environment away from the host and are thus expected to be affected by changes in climate. Most empirical and theoretical studies demonstrate or predict range shifts or increases in ticks and tick-borne diseases, but there can be a lot of heterogeneity in such predictions. Tick-borne disease systems are complex, and determining whether changes are due to climate change or other drivers can be difficult. Modeling studies can help tease apart and understand the roles of different drivers of change. Predictive models can also be invaluable in projecting changes according to different climate change scenarios. However, validating these models remains challenging, and estimating uncertainty in predictions is essential. Another focus for future research should be assessing the resilience of ticks and tick-borne pathogens to climate change.

INTRODUCTION

Pathogens that are transmitted by direct or close contact can spread amazingly rapidly through a susceptible population, as we experienced with the novel coronavirus (SARS-CoV-2, which causes the disease COVID-19), which spread around every country on the globe extremely rapidly in 2020, a consequence of modern globalization, especially international travel. However, vector-borne pathogens, particularly those transmitted by slow-reproducing, multistage, slow-feeding, largely immobile vectors, such as ticks, do not have the capacity for such rapid spread. Nevertheless, several tick species and the pathogens that they carry are currently increasing in distribution and incidence, with serious consequences for human and animal health and welfare. The reasons for these changes may be multiple, inter-related, and complex; this review focuses on discussing the evidence concerning whether climate change parameters are important drivers of the reported changes in abundance or distribution of key tick species and tick-borne diseases.

The Global Importance of Ticks and Tick-Borne Diseases

Ticks are members of the Acari family, related to spiders and mites, and are globally important as disease vectors, carrying more types of pathogens of humans and livestock than any other invertebrate vector (13, 36, 66). Many of these pathogens cause serious health, welfare, and economic issues. For example, Lyme disease, caused by the *Borrelia burgdorferi* sensu lato complex of spirochete bacteria, is the most prevalent vector-borne disease in the Northern Hemisphere, occurring throughout temperate regions of North America, Europe, and Asia. Various other species of *Borrelia* cause a range of tick-borne relapsing fevers in many tropical and subtropical countries, as well as some parts of North America; these fevers cause death in up to 10% of untreated infected people (e.g., 19). The tick-borne encephalitis (TBE) complex of viruses, which is endemic in much of Europe and across Asia, also has a mortality rate of up to 10% (17). The many species of *Rickettsia* cause spotted fevers throughout the Americas (from Canada to Brazil), Asia, the Mediterranean region, Africa, and tropical Northeastern Australia. Other tick-borne diseases include: babesiosis, bartonella, and a range of ehrlichioses and anaplasmoses globally; Q fever, caused by *Coxiella burnetii*, which is widely distributed globally; tularaemia, caused by *Francisella tularensis*, which occurs in Europe, Japan, North America, and the former USSR; the viral Crimean-Congo hemorrhagic fever, which causes 10–50% mortality (20, 84); and the Banyangvirus (SFTS virus) of eastern Asia.

Ticks are enormously widespread globally, occurring on all continents, including Antarctica [*Ixodes uriae*, the seabird tick (5)]. Ticks comprise approximately 800 species (650 Ixodidae hard ticks and 150 soft ticks), many of them specializing on particular types of host (e.g., *Ixodes lividus*, the sand martin tick, which lives in sand banks along the nesting tunnels of sand martins). The majority of tick species are under studied, so it is impossible to discuss the potential impact of climate change on most tick species and the pathogens that they vector. In this review, therefore, most of the information is drawn from the most extensively studied tick species, which tend to be the most important in terms of transmission of prevalent tick-borne pathogens and are often generalists in terms of hosts; moreover, most of the literature on climate change implications is from North America and Europe. The types of tick that are most important in terms of abundance, distribution, and contribution to tick-borne disease, as well as being the best studied, include *Ixodes ricinus* throughout Europe; *Dermacentor reticulatus* and *Ixodes persulcatus* in Siberia and Asia; the black-legged tick *Ixodes scapularis* in much of the eastern half of North America; *Ixodes cookei*, the most abundant tick in Quebec; the Rocky Mountain wood tick *Dermacentor andersoni* in North, Central, and South America; Amblyomma ticks, which dominate South America [especially *Amblyomma neumanni*, *Amblyomma cajennense*, *Amblyomma trieste*, *Amblyomma ovale*, and *Amblyomma aureolatum* (30)]; and the paralysis tick *Ixodes holocyclus* in Australia.

Climate Envelopes

All organisms that interact with the external environment exist within their own climate envelope, which defines the climatic conditions under which their populations can survive. Some ticks have a narrow climate envelope, requiring specific climatic conditions; this is likely to result in a fairly narrow geographic distribution such that changes in climatic conditions are more likely to impact the population size and range of such species than for ticks with wider distributions. Conversely, some tick species have huge geographic distributions, as is the case for *I. ricinus*, which is an abundant generalist tick feeding on almost any terrestrial vertebrate across almost all of Europe, as well as other regions (52). It ranges from Arctic Norway in the north to North Africa in the south, from the northeast Atlantic seaboard in the west to the Caspian Sea in the east (26), and from sea level to 1,500 m elevation in the European Alps, demonstrating an astonishingly wide climate envelope. Similarly, *I. scapularis*, another generalist feeder, is estimated to range across almost the entire eastern half (or at least third) of the United States and into Canada (18). For species like this, climate change is likely to have direct effects primarily at the far edges of its latitudinal and altitudinal range. In addition, species such as these with wide climate envelopes and geographic ranges have clearly adapted to local climates and to local host communities; thus, they may potentially have the ability to adapt and show resilience to current climate changes (28). Generalist ticks such as *I. ricinus* and *I. scapularis* are more likely to be able to shift their ranges due to climate change, rather than suffer range contractions, as they may be able to utilize new hosts; for example, they may shift from red deer, *Cervus elaphus*, or white-tailed deer, *Odocoileus virginianus*, to reindeer (caribou), *Rangifer tarandus*.

Indirect Effects of Climate Change

Climate change may also operate indirectly on tick distribution and abundance via changes in hosts. Again, for generalists such as *I. ricinus* and *I. scapularis* that can feed on almost any land animal, climate-induced changes in hosts are less likely to have a large impact. However, for ticks that are more host-specific, such as the long-legged bat tick *Ixodes vespertilionis*, if climate change impacts host populations, then we might expect the indirect effect on the ticks to be dramatic.

Difficulties in Inferring Climate Change as a Driver

In practice, it can be extremely challenging to tease apart the mechanisms for changes in distribution and abundance of ticks and tick-borne disease, i.e., whether these changes are due to the climate per se changing or due to climate-related changes in hosts, habitat, or even human behavior that alter the risk of exposure (**Figure 1**). It is important to remember, too, that changes in hosts, habitat, and human behavior often occur irrespective of climate. This makes it even more difficult to determine whether a change in tick-borne disease, due to a change in, for example, hosts, is ultimately related to climate change at all, or instead is related to other drivers that have changed host abundance, such as anthropogenic land use or wildlife management.

To demonstrate climate change impacts on tick populations and tick-borne disease risk and incidence, long-term data sets are required from the same areas, and these are not common. Even where such data sets exist, merely showing a correlation between a changing climate and a change in tick population or tick-borne disease incidence does not imply causation. If the correlation is coupled with additional data demonstrating tick responses to the appropriate climate parameters while also showing no consistent changes in other potential drivers (such as hosts), then one could potentially infer that climate change is responsible. Models of ticks, tick-borne disease, climate, habitat, and hosts can also help us infer (but not prove) potential drivers. Various types

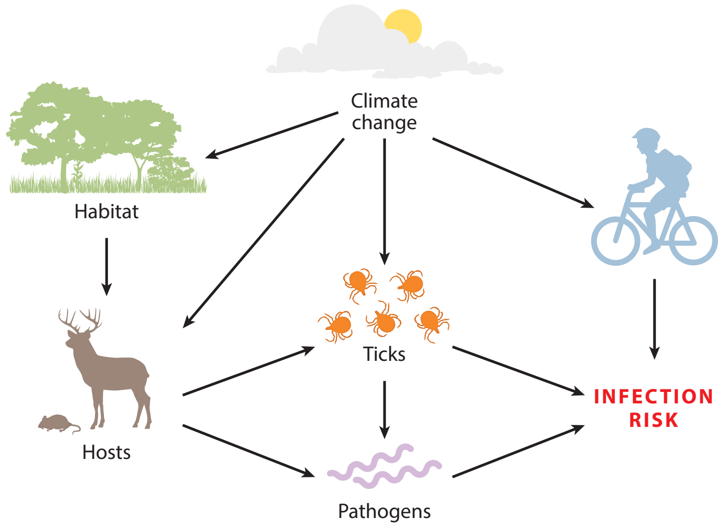

Figure 1

Schematic diagram showing how climate change can affect ticks directly (by changing oviposition, development, mortality rates, and activity) and indirectly (by changing habitat and host species and abundance). Climate change can, in turn, affect tick-borne pathogen infection risk in humans by directly affecting human behavior (e.g., outdoor recreation) and indirectly affecting pathogen transmission rates and prevalence via hosts and ticks. The relative importance of each pathway is challenging to ascertain.

of predictive models are also often used to project how climate change (and other changes) might impact ticks and tick-borne disease risk, based on our current knowledge of tick or disease life history responses to climate parameters (e.g., activity and mortality related to temperature) or current climate-related abundances or distributions.

Mechanisms for Climate Change Impacts on Ticks and Tick-Borne Diseases

The most recent estimates of climate change indicate that, globally, the climate has warmed by an average of 1°C since the preindustrial period (1850–1900), and temperatures are projected to exceed 1.5–2°C by 2081–2100 (33). However, climates are not changing in the same way over the globe; for example, temperatures are increasing more over land than over the oceans, and areas of the Arctic are projected to experience much higher temperature rises than most other regions (33). It is not only temperature that is changing; rainfall is also changing, with some areas receiving more rainfall or more extreme weather events (e.g., heavier rainstorms, higher winds, and more frequent flooding events), while other areas, especially drier regions, experience more prolonged and frequent droughts.

Because ticks spend most of their lives off the host, they are subject to abiotic environmental conditions and are likely to be affected by all of these climate change parameters. For example, it has been demonstrated for *I. ricinus* that warmer temperatures speed up oviposition rates, egg development rates, and interstadial development rates (45, 51, 71). Experiments demonstrate that a higher proportion of the *I. ricinus* population is active at warmer temperatures (28). Several studies have shown how saturation deficit (the drying power of the air, a function of both temperature and relative humidity) affects *I. ricinus* activity (e.g., 65, 69). Thus, for ticks with similar environmental needs to *I. ricinus*, the colder edges of the climate envelope are most likely to be set by cool temperatures inhibiting life cycle rates and activity. Increased winter mortality at higher altitudes and latitudes may also play a role in setting the climate envelope, as *I. ricinus* cannot survive long in temperatures below −15°C (51). Further south, where there are warmer temperatures, *I. ricinus* ticks benefit from higher life cycle rates and activity, but when temperatures reach above 30°C (even if the humidity is high, i.e., >80%), they experience much greater mortality; this is thought to set the southern limits to their range (51). Tick abundance per se can be relevant to pathogen transmission rates: With higher tick densities, there is an increased likelihood of more ticks biting (and therefore acquiring infection from) a host while it is infectious (**Figure 2**).

In addition to the effects of climate parameters on tick development, oviposition, fecundity, mortality, and activity, climate may change the seasonal phenology of the different tick stages (larvae, nymphs, adults). This can be relevant to disease risk when pathogen transmission requires infected nymphs to feed on a host simultaneously with uninfected larvae, e.g., through nonsystemic cofeeding transmission (**Figure 2**), as is the case with TBE virus (42). If the seasonal peak of larvae coincides with the peak of nymphs, then more larvae will become infected. Therefore, if climate change shifts the seasonal peaks of the different tick stages one way or the other, then disease transmission potential may change (72).

Even where climate change does not directly affect tick demographics, climate change may affect habitat and host abundance, with cascading effects on tick abundance and pathogen prevalence (**Figure 1**). It is not necessarily difficult (if the data exist) to determine a link between changes in habitat, land use, or host abundance and tick and tick-borne disease incidence. However, it can be difficult to determine whether the ultimate driver for these indirect effects is climate related and, if so, the extent to which climate's impact is greater than those of other potential drivers.

COMPARISON OF RELEVANT TICK AND DISEASE PARAMETERS

Climate change may affect the geographic distribution (i.e., presence or absence) and/or the abundance of ticks. Abundance is a more useful and interesting parameter both ecologically and in terms of risk of exposure. However, most tick survey methods (e.g., counting tick burdens on hosts, flagging or dragging blankets or cloth material over vegetation, or using means such as carbon dioxide traps) count only active ticks, and tick activity can vary hugely depending on season and immediate weather conditions; moreover, methods vary between studies. Therefore, although active tick abundance should be, theoretically, the gold standard for measuring impacts of climate change, many empirical and theoretical studies use distribution (presence or absence within a geographical area). This parameter is less sensitive to change and will miss a lot of detail, but it is less prone to error both within and between studies and is easier to model.

The parameters used for assessing risk of tick-borne diseases also need to be clarified. The most important parameter from the human perspective is disease incidence, the recorded number of people diagnosed with infection per unit population, e.g., per 10,000 people in a defined area. A key parameter from the tick ecology perspective is the density of infected ticks (usually nymphs) in the environment. This is often used as a proxy for risk to humans. A further parameter, which is less useful in terms of human exposure because it does not include active tick density, is pathogen infection prevalence in ticks (the proportion of ticks testing positive for infection with the pathogen). This is of academic interest to those seeking to understand the role of different host types in driving pathogen transmission cycles. These parameters may have differing responses to climate change because some include tick activity and survival only, some also rely on host types and densities, and disease incidence also contains a human density and behavior component. It is therefore important to recognize which parameter is under scrutiny during climate change studies.

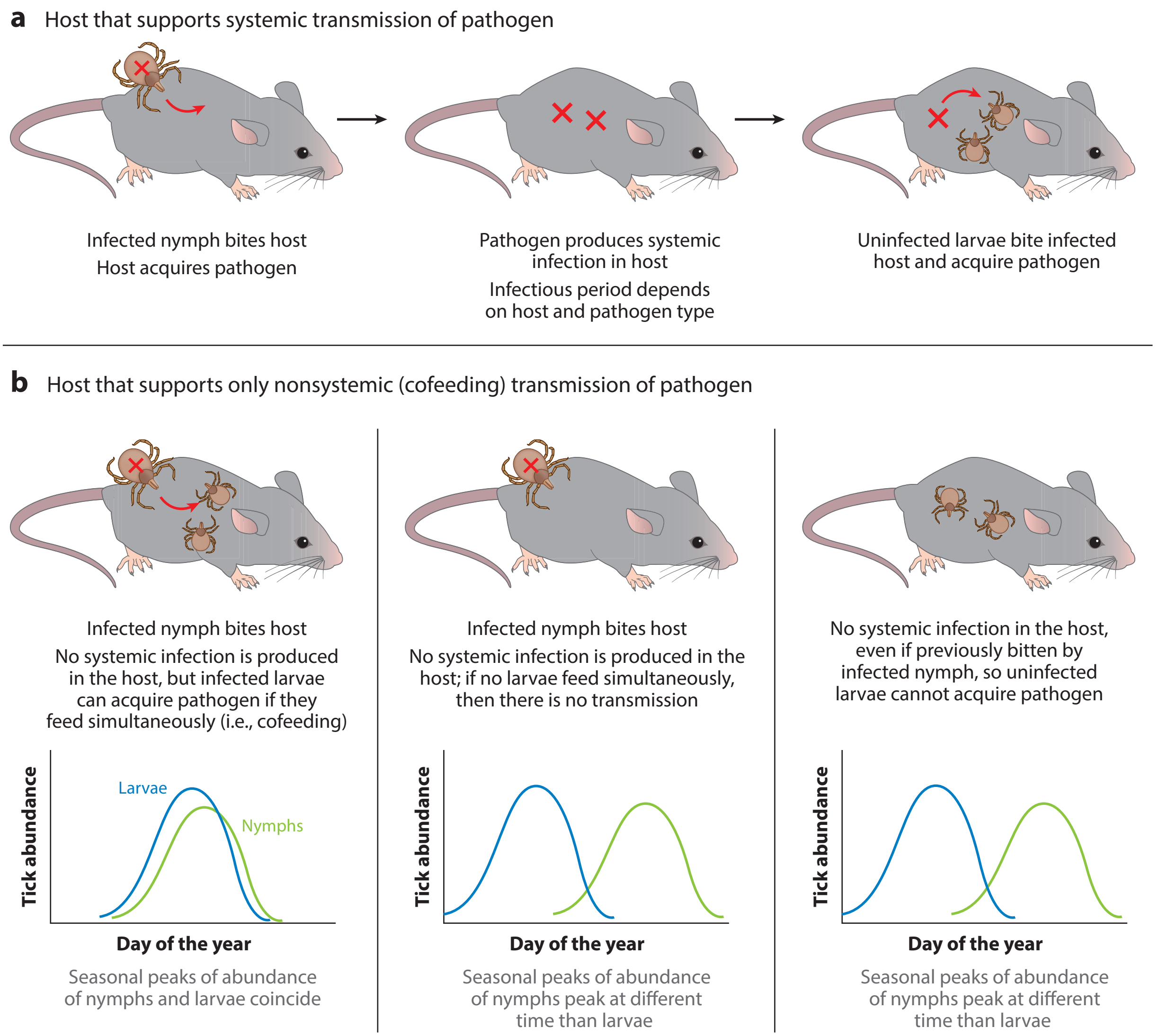

Figure 2

Schematic diagram illustrating potential ways in which climate change may affect pathogen transmission. (*a*) Hosts that support systemic transmission allow the pathogen to multiply systemically after an infected tick bite. The infectious period depends on the pathogen and on the host species and its immune status. If uninfected ticks bite the host while it is still infectious, then the pathogen can be transmitted to the ticks. If climate change were to increase the tick density (directly or indirectly), then it would become more likely that more ticks will bite the host while it is still infectious, thereby increasing the number of infected ticks. (*b*) Some hosts that do not produce a systemic infection can still support transmission nonsystemically if ticks feed simultaneously and close together (termed cofeeding). For many tick-borne pathogens, there is no (or only rare) transovarial transmission, meaning that larvae that have yet to feed are uninfected. Nymphs, however, may be infected and can pass the pathogen through the skin of the host (thus bypassing the host's blood system) to cofeeding larvae. This is most likely to occur when the climate is such that the seasonal peaks of abundance of nymphs and larvae coincide (*left*). If climate change were to cause the abundance of nymphs to peak at a different time to that of larvae (*right*, *middle*), then cofeeding transmission would occur less frequently (42).

The above caveats about the difficulties of discerning climate change effects versus those of hosts, habitat, or humans, and the errors in measuring the various relevant parameters (tick presence, tick abundance, disease incidence, or pathogen prevalence or risk), must temper any conclusions about climate change's impacts on tick-borne disease. In the following section, I consider what actual evidence there is for changes in abundance or distribution of ticks and tick-borne pathogen risk in relation to climate change.

EVIDENCE FOR CLIMATE CHANGE IMPACTS OVER SPACE: ALTITUDE STUDIES

Long-term studies are essential for measuring long-term changes, such as those due to climate change; however, these studies are rare. However, for inferring the impact of climate change, altitude is a useful surrogate because the climate changes spatially rather than temporally, and altitude includes changes in habitat and hosts that would likely accompany long-term temporal climate change. Moving to a lower altitude simulates climate warming: There is typically, on average, a rise in approximately 6.5°C for every 1,000-m drop in elevation (4). Using *I. ricinus* as an example, interstadial development, oviposition, and egg development are faster in warmer temperatures (50, 71), and the proportion of ticks that are active increases [up to a point and provided that relative humidity remains adequate (e.g., 28, 65, 69)]. It is not surprising, therefore, that many studies have demonstrated that *I. ricinus* abundance increases as elevation drops (i.e., with spatial climate warming) (2, 6, 7, 27, 38, 67). Furthermore, as we would expect, the altitudinal limit depends on the climate of the country. For example, in the colder, northern part of the range of *I. ricinus*, the altitudinal limit is approximately 500 m above sea level in western Norway (37, 67) and 600 m in northeastern Scotland (27), rising to 1,100–1,500 m further south, in northern Italy, Switzerland, and the Czech Republic (6, 8, 14, 54, 73), and as high as 2,000 m in Spain (56).

Similarly, several studies report higher *B. burgdorferi* sensu lato prevalence at lower altitudes (35, 38), although others found no effect (8). The more relevant parameter for infection risk to humans, i.e., the density of infected *I. ricinus* nymphs, also increases with a drop in elevation, i.e., warmer climate (e.g., 35, 73). If a drop in altitude really is a good surrogate for a warming climate (in the long term, after habitat and hosts have also changed), then these studies suggest that *I. ricinus* populations and Lyme disease risk may increase with climate warming, at least in cool, temperate northwestern Europe and at higher altitudes.

EVIDENCE FOR CLIMATE CHANGE IMPACTS OVER TIME

Attributing long-term range shifts or changes in abundance to climate change is fraught with difficulty, as other changes are likely to have taken place during the period under examination [e.g., changes in habitat, hosts, and anthropogenic factors (40, 70)]. Semenza & Suk (76) point out that climate change is probably a factor in the recent emergence in Europe of several exotic vector-borne diseases (such as West Nile virus) and vectors (such as the mosquito *Aedes albopictus*, which vectors Zika virus, dengue fever, and chikungunya); however, other vector and disease range expansions are due to increasing globalization and international air travel, not climate change. What evidence is there for changes in incidence or distribution of ticks and tick-borne diseases, and can we conclude that the main driving force behind these changes is climate change?

Evidence for Climate Change Impacts on Ticks

For some range shifts, climate change does seem to be at least one of the key drivers; this is particularly likely to be the case at the edges of the altitudinal and latitudinal range of the tick and pathogen in question, where climate is a limiting factor. For example, *I. ricinus* has displayed a range shift northwards in Europe, its northern limit now being 69° N in Arctic Norway, which is a 400-km northward shift since the 1940s (37); similarly, in Sweden, *I. ricinus* has spread from below 61° N to 66° N since the 1980s (48, 81). *I. ricinus* is also shifting upwards in altitude; for example, in the Czech Republic, the upper altitudinal limit has increased from approximately 700 m in the 1950s to 1,100 m in the 2000s (15, 54). Increases in distribution and abundance of *I. ricinus* in the United Kingdom (41, 75) are, however, also likely to be linked to substantial increases in the distribution and abundance of deer (12, 56), which are the primary reproduction host for *I. ricinus* in the United Kingdom (29). However, the increase in red deer in Scotland may be related to changes in winter weather conditions (12), so there may also be an indirect influence of climate change on *I. ricinus* in the United Kingdom. A mechanistic, agent-based model predicted that *I. ricinus* would expand its activity season and altitudinal range in Scotland due to climate warming, resulting in an increase in Lyme disease risk, even within the bounds of the climate envelope (45). Ecological niche modeling also predicts a range expansion of *I. ricinus* further north and east in Europe as a result of climate change (1).

Similarly, in Canada, a suite of increasingly refined mechanistic and dynamic models of *I. scapularis* life stages predicts that, under scenarios of climate warming, there will be higher population survival and range expansion beyond the current climate envelope into cooler regions of Canada (55, 61–63, 88).

The lone star tick, *Amblyomma americanum*, is common in the southeastern United States and is a threat to human health, as it vectors *Ehrlichia* and *Rickesttsia* species and *F. tularensis* (for a review, see 80). Records show that *A. americanum* has expanded north to the Canadian border since the 1890s (80); while the reason for this expansion is not known, the distribution matches predictions from dynamic population models based on temperature suitability (74). These models also predict that climate change will cause further northerly range expansion into colder parts of Canada (74).

While most empirical studies and theoretical predictive models suggest range expansions of ticks due to climate change, some ticks may experience the opposite. For example, climate suitability models of the *Amblyomma cajannense* species complex in Brazil predict a contraction in range under future climate scenarios (64), with positive health implications for spotted fever in the region.

Focusing not only on thermal climate change, but also on rainfall, in Argentina and Australia, climate and habitat suitability models predict increases (at least in some areas, especially where rainfall is projected to increase) of the cattle tick *Boophilus microplus*, with negative implications for the beef cattle industry (21, 86).

What is good for one species of tick may not be good for another. While *I. ricinus* and *I. scapularis* require low saturation deficit for survival and activity (65, 69), such that climate warming is shifting these tick species further north, some ticks benefit from hotter, drier climates. For example, some of the Argasid soft ticks of the *Ornithodoros* genus are adapted to hot, dry climates, and *Ornithodoros sonrai* and *Ornithodoros marocanus* have increased in abundance and distribution in Senegal and northwest Morocco due to more frequent droughts (a manifestation of climate change) in these regions (78, 83).

Evidence for Climate Change Impacts on Tick-Borne Diseases

An increase in tick abundance or distribution does not necessarily translate directly into increases in pathogen prevalence, disease risk, or disease incidence, which also depend on densities of transmission hosts. What is the evidence for climate change–induced shifts in tick-borne diseases?

Lyme disease. Reported cases of Lyme disease have increased fourfold (from approximately 10,000 to 40,000) in the United States since the early 1990s (9). There is little evidence that climate change is the main driver of the emergence of Lyme disease in northeastern regions of the United States, which are well within the climate envelope of the main vector, *I. scapularis*; instead, the increase has been attributed to a recovery in white-tailed deer, *O. virginianus*, populations driving an increase in tick densities (e.g., 3, 79, 87) and, interestingly, to changes in predator abundance (specifically an increase in coyotes, *Canis latrans*, causing a decrease in red foxes, *Vulpes vulpes*), which has resulted in an increase in densities of the small mammals that transmit *B. burgdorferi* sensu lato (44).

However, at the northern edge of the climate envelope, the increase in cases of Lyme disease in Canada (most cases are in Ontario) (59), while also having multiple drivers (85), is thought to be driven largely by a climate change–induced northern range expansion and increased densities of black-legged ticks, *I. scapularis* (11); this is in line with multiple model predictions of a warming climate (e.g., 10, 43, 77). Models by McPherson et al. (55) predicted that Lyme disease will further increase substantially under most climate change scenarios in many parts of southern Canada, and that it will increase (albeit to a lesser degree) under even the most optimistic greenhouse gas emissions scenarios.

In Europe, as well as in North America, the probable drivers for the reported increases in Lyme disease vary depending on the proximity to the edge of the vector's climate envelope and on what other environmental or anthropogenic changes have been occurring. For example, reported cases of Lyme disease in Scotland increased dramatically over a 10-year period, from a mere handful in the late 1990s to approximately 300 annually from 2008 to the present time (31). However, with the vector *I. ricinus* and the *Borrelia* transmission hosts being well within their climate envelope in Scotland, it is likely that this increase is not driven directly or primarily by climate change. The increase in reported incidence of Lyme disease in Scotland (and the rest of the United Kingdom) could potentially be due to a combination of improved awareness and diagnostics, more people enjoying outdoor recreation, and a reported increase in *I. ricinus* populations (41, 75), which may relate to a threefold–fourfold increase in deer abundance since the 1960s (e.g., 12). There may, however, be an indirect climate component to the rise in *I. ricinus* in Scotland, since the increase in deer is thought to have been influenced in part by milder winters (12).

However, in the northern extremities of its European range, such as in northern and inland Norway, anthropogenic factors are considered to be not such an important driver of the reported increase in Lyme disease cases (37). Instead, in northern and inland Norway, similar to the situation in Canada, it is likely that climate warming has played a stronger role in the increase in Lyme disease cases (37). In Norway, Mysterud et al. (57) demonstrated a temporal and spatial positive association between Lyme disease cases and deer density; however, their analysis suggested that climate warming may have also played a role in the recent emergence of Lyme disease cases in Norway.

Predictive models of Lyme disease and climate change reflect the complexity of the system and rarely give simple predictions. For example, Li et al. (46) predicted that Lyme disease risk across Europe will increase under certain combined climate change and anthropogenic change scenarios in some areas but will remain unchanged or decrease in others.

Tick-borne encephalitis. Cases of TBE have increased in Europe by approximately 400% in the past three decades (25). Randolph (70) argued that the reasons for the surge in cases of TBE in Europe were highly complex and multifactorial, including sociopolitical changes leading to changes in human behavior, which increased exposure of humans to infected ticks. However, at the altitudinal and latitudinal edges of the range of TBE virus, climate change has been implicated in the expansion of *I. ricinus* ticks and TBE virus to higher altitudes in the Czech Republic (16, 90) and Slovakia (49) and northward in Sweden (47, 48). An insightful review by Jaenson et al. (34) showed that human cases of TBE in Sweden had steadily increased 10-fold in a 30-year period since the 1980s, and they concluded that this was most likely due to changes in host abundance, with climate playing a complex and indirect role, acting via hosts, habitat, and human behavior. For example, roe deer (that do not transmit TBE virus) abundance decreased during this period, which was, in some years, due to winter weather causing high mortality; because of this decrease, more ticks had to feed on rodents (transmission hosts). Warmer, more humid summers in some years improved ground vegetation habitat and tick activity and survival while also encouraging more people to spend more time outdoors. In addition, in some years, higher summer rainfall increased the number of fruiting bodies of fungi, which people collected, exposing themselves to ticks in the woodlands. This is an excellent example of how climate change may affect tick-borne disease risk through its impact on the many other factors relevant for the transmission cycle and human exposure, which makes assigning a relative importance to each factor extremely difficult (see **Figure 1**).

Models (68, 72) predict that TBE virus will increase at higher altitudes and latitudes, as the empirical data also suggest; interestingly, however, models also predict a contraction of TBE virus in parts of the current main range, such as Switzerland and Hungary. The models suggest that this is due to climate change altering the phenology of the different stages of *I. ricinus* such that the seasonal peaks of larvae and nymphs no longer coincide, thus disrupting the transmission cycle on rodents, which are the main competent hosts that allow nonviremic transmission between cofeeding ticks (42). Robust validation of models that predict the future is not possible (until time has passed), and some models that also take into account the phenology of different tick stages predict that TBE virus transmission will increase substantially within the current range [e.g., for Hungary (58)]. Two key issues that require more attention are the creation of uncertainty estimates for and validation of such predictive models.

Climate change may have other impacts in addition to those on range shifts and incidence rate changes. For example, TBE virus exhibits large interannual variations in prevalence and incidence related to interactions among host population cycles, host immunity, and longevity. Zeman (89) demonstrated cyclical oscillations in TBE virus in large areas of Europe (Sweden, Germany, the Czech Republic, Slovenia, Austria, and Italy) and showed that climate change alters the length of these cycles: Warmer conditions lengthen the cycle frequency due to increased host longevity reducing the speed of variation in host immunity, which feeds back into the level of TBE virus circulating in the host (and tick) population.

Crimean-Congo hemorrhagic fever. Crimean-Congo hemorrhagic fever, vectored by the *Hyalomma* genus of ticks, is endemic in the Middle East, the western half of Asia, and parts of Africa (53). In the past 20 years there have been increased cases and outbreaks in parts of eastern Europe (Ukraine, Greece, Albania, Kosovo, southwestern Russia, and Turkey) (for a review, see 53). Models of climate and habitat for Turkey suggest a role of climate change, since this rise in cases is associated with increased climate suitability for the *Hyalomma* tick vector, as well as with anthropogenic factors such as fragmentation of agricultural land (24). *Hyalomma marginatum*, the main tick vector of Crimean-Congo hemorrhagic fever in Europe, is endemic to some areas of southeastern Europe, and models also predict that climate change (increased temperature and reduced rainfall) will increase *H. marginatum* populations in the Mediterranean region and cause a range expansion to the north (23). Indeed, there are already records of *H. marginatum* in the Netherlands and southern Germany (22, 39, 60).

Tick-borne relapsing fever. Tick-borne relapsing fever is caused by various species of *Borrelia* spirochete bacteria. It is one of the most prevalent bacterial diseases in Africa; in parts of Senegal, it has increased in incidence since the 1970s, and there has been an estimated 350-km range expansion into northwest Morocco, apparently in response to increasing drought conditions (78, 83). The mechanism behind these changes is an increase in populations of the *Ornithodoros* tick vectors (*O. sonrai* and *O. marocanus*) that benefit from arid conditions, thereby increasing transmission of the pathogens *Borrelia crocidurae* and *Borrelia hispanica* in the rodent transmission hosts (78, 83).

RESILIENCE TO CLIMATE CHANGE?

Climate change, like any other major ecological or external change experienced by organisms, is likely to impose new selective pressures on parasites and pathogens. This could result in either adaptation to the new climate, new hosts, or new habitat, which could lead to new strain types, races, or even species of vectors or pathogens; alternatively, if they do not adapt, it is possible that local extinction of the vector or pathogen could occur (for a review, see 32). Resilience can have different meanings in different fields and contexts. In this case, resilience refers to the ability of a tick species or pathogen to survive and maintain a viable population when exposed to a change in climate. This may require the ability to adapt (through genetic evolution or phenotypic plasticity) to the new environment.

There is very little information on resilience of ticks or tick-borne diseases to changing climates, and there is even a paucity of information on how ticks might be able to adapt to certain parameters of climate, such as temperature changes. This would be an important area of research to conduct because modeled projections of changes in tick populations and tick-borne disease incidence due to climate change do not generally consider adaptation in the climate capabilities of ticks, their habitats, or their hosts. However, if ticks are able to adapt to changing climates, then there is the possibility that model projections of change that are based on current tick temperature responses may be too strong. For example, Gilbert et al. (28) and Tomkins et al. (82) conducted experiments using *I. ricinus* from contrasting climates (northeastern Scotland, Wales, southern England and south-central France) and demonstrated that the proportion of *I. ricinus* that are active substantially increased with rising temperatures for all populations. However, importantly, the exact pattern of increasing activity with temperature differed between populations: Ticks from the warmer climate of south-central France were better adapted to warmth than were ticks from cooler climates further north; for example, at 7°C, fewer than 10% of French ticks were active, compared to almost 40% of Scottish ticks (28). These experiments clearly demonstrate that *I. ricinus* adapts its activity to its local thermal climate, although it is not known whether this adaptation is a result of intergenerational genetic evolution or phenotypic plasticity (including maternal effects). The mechanism of adaptation is relevant in the context of climate change resilience because adaptation due to phenotypic plasticity occurs very quickly (within the same generation or, for maternal effects, the next generation), whereas genetic evolution generally takes many generations. Depending on the mechanism and speed of adaptation, therefore, when climate warming disposes Scotland in the future to have a similar thermal climate to that of France in the present, Scottish ticks may no longer display such high activity at cooler temperatures. Instead, we might expect them to display reduced activity, like French ticks currently do, thereby reducing exposure risk to humans and buffering the impact of climate change.

FUTURE ISSUES

In terms of optimizing the approach to disease control and mitigation, it is crucial to be able to distinguish the effects of climate change from those of other drivers of tick-borne disease change (such as changes in populations of deer, rodents, and predators or in human behavior). For example, if disease increase is due to a rise in deer densities, then controlling deer densities could be considered as a mitigation strategy (29). However, if the primary cause of disease increase is climate change, then a different part of the disease cycle needs to be targeted (such as by mitigating human exposure through awareness campaigns or improving postinfection treatment through practitioner education). Predictive models projecting changes in ticks and tick-borne disease risk due to climate change are becoming more refined, but without validation data sets (which are impossible until time has passed), it is crucial to focus on estimates of uncertainty in the predictions (64). Future research should also incorporate the idea of resilience to climate change through adaptation of ticks and hosts to local conditions, and the extent to which ticks and pathogens are able to utilize new hosts outside of the current climate envelope.

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