Biologia (2022) 77:1503–1512
https://doi.org/10.1007/s11756-021-00927-2

REVIEW

Climate change impacts on ticks and tick-borne infections

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Received: 1 July 2021 / Accepted: 30 September 2021 / Published online: 23 November 2021

Abstract

Evidence climate change is impacting ticks and tick-borne infections is generally lacking. This is primarily because, in most parts of the world, there are no long-term and replicated data on the distribution and abundance of tick populations, and the prevalence and incidence of tick-borne infections. Notable exceptions exist, as in Canada where the northeastern advance of *Ixodes scapularis* and Lyme borreliosis in the USA prompted the establishment of tick and associated disease surveillance. As a result, the past 30 years recorded the encroachment and spread of *I. scapularis* and Lyme borreliosis across much of Canada concomitant with a 2-3 °C increase in land surface temperature. A similar northerly advance of *I. ricinus* [and associated Lyme borreliosis and tick-borne encephalitis (TBE)] has been recorded in northern Europe together with expansion of this species' range to higher altitudes in Central Europe and the Greater Alpine Region, again concomitant with rising temperatures. Changes in tick species composition are being recorded, with increases in more heat tolerant phenotypes (such as *Rhipicephalus microplus* in Africa), while exotic species, such as *Haemaphysalis longicornis* and *Hyalomma marginatum*, are becoming established in the USA and Southern Europe, respectively. In the next 50 years these trends are likely to continue, whereas, at the southern extremities of temperate species' ranges, diseases such as Lyme borreliosis and TBE may become less prevalent. Where socioeconomic conditions link livestock with livelihoods, as in Pakistan and much of Africa, a One Health approach is needed to tackling ticks and tick-borne infections under the increasing challenges presented by climate change.

Keywords Climate change · Tick range expansion · Tick-borne pathogen · Lyme borreliosis · Tick-borne encephalitis · Tick and disease modelling

Introduction

Global mean land surface temperature has increased by 1.5 °C since pre-industrial times (Allen et al. 2018). However, in many regions, and during many seasons, warming on land has been greater than the global average. This has been particularly noticeable in the Arctic region, e.g. on June 2020, 38 °C was recorded at a Siberian weather station where 20 °C is considered normal (WMO 2020). Change is most apparent during the Arctic winter; in Alaska and western Canada, average winter temperatures have risen by 3-4 °C in the past 50 years (Černý et al. 2021). The Earth's rising temperature is driven primarily by increasing concentrations of greenhouse gases in the atmosphere, particularly carbon dioxide, methane, and nitrous oxide, resulting from human activities (Myhre et al. 2014). Warming forces from greenhouse gases are partially counterbalanced by particulate pollution, especially sulphate aerosols which reflect sunlight directly and make clouds brighter and more reflective. Future predictions of climate change differ some twofold primarily because of uncertainties in the contribution from clouds in future global and regional warming (Bellouin et al. 2019). Nevertheless, there is general agreement the Earth is undergoing human-induced warming resulting in the increased frequency and magnitude of heatwaves, heavy precipitation events, and droughts (Allen et al. 2018).

There is even greater uncertainty in assessing whether changes in climate are affecting ticks and tick-borne infections. Because ticks are poikilothermic, comparatively long-lived (some species taking >5 years to complete one generation), and generally spend most of their life cycle off-host, environmental conditions greatly influence their physiology and behaviour (Apanaskevich and Oliver 2014). A critical requirement for tick survival is water (or water

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retention). Ixodid ticks produce hygroscopic secretions from their salivary glands to absorb atmospheric water vapour while argasid ticks have a specialized lipid layer that helps conserve water (Knulle and Rudolph 1982). Blood is also critical for tick survival, providing nutrients for development and egg laying. Although most tick species will feed on any available vertebrate, they tend to show a preference linked to whether they are exophilic or endophilic, generalists or specialists. Climate change is expected to impact ticks (and tick-borne infections) through climate-induced changes in environmental conditions and host availability. However, unequivocal evidence ticks (let alone, tick-borne pathogens) are being affected by climate change is limited. This is because there are so many confounding factors which, for tick-borne pathogens, are compounded by the complexity of the tick-host-pathogen triangle of interdependent interactions. The following brief review attempts to summarise evidence climate change is impacting ticks and tick-borne infections, and considers predictions for the future.

Signals of change

Most countries and regions of the world have not recorded any influence of climate change on ticks and/or disease incidence/prevalence. This is often because, in many countries/regions (e.g. Africa, Australia, China, India, Japan, Pakistan, Taiwan, the Arctic, the Middle East), long-term replicated data on tick distribution, prevalence, and abundance are not available, diseases caused by tick-borne pathogens are not notifiable, and basic knowledge of tick-host-pathogen interactions is lacking (Nuttall 2021). In other cases, socio-economic change may overwhelm any climate-induced signal of change. One example is in Russia where tick-borne encephalitis (TBE) cases in humans hit their highest record (6.8/100,000) in 1999, subsequently declining. This peak coincided with a period of increased contact of city dwellers with ticks, a consequence of a legislative change allowing undeveloped land to be used for suburban housing and garden plots (allotments), which increased 3- to 5-fold between 1980 and 1995 (Korenberg 2009). Another example is in the USA, where the remarkable range expansion of *Ixodes scapularis* Say, 1821 during the past 50 years may simply reflect reclamation of territory once inhabited by this notorious vector before settlers cleared land for agriculture, fuel, and construction, and hunted deer (the reproductive host for *I. scapularis*) for food and leather (Hoen et al. 2009).

If recent changes in the Earth's climate are affecting ticks/tick-borne infections, one or more signals of change should be apparent in: (i) geographical distribution; (ii) development rate; (iii) phenology (seasonal activity) of ticks; (iv) tick phenotype/genotype; (v) tick microbiota. Ideally, long-term and replicated field studies are needed to detect the impact of climate change on ticks, the infections they transmit, and the microbiota they carry. There are many challenges, not least being how long is 'long-term,' how to sample without confounding the results, sampling frequency, and where to locate field studies (bearing in mind vegetation changes over time). Even a 35-year replicated study monitoring *Ixodes ricinus* Linnaeus, 1758 questing populations in the Tula region of Russia could not distinguish between climate change and human influence on the observed increase in tick abundance during the latter 21-year period (Korotkov et al. 2015). A continuous 6-year study of questing *I. ricinus* in the Czech Republic detected a climate signal in the long-term dataset for TBE: extreme meteorological events coincided with an anomaly in the correlation between annual number of TBE cases and number of active nymphs (Daniel et al. 2018). However, such studies can only ever be correlative just as the causes of Anthropocene climate change are correlative even though the probability of a human-induced cause is high.

Expansion in geographical distribution of ticks and tick-borne infections

Perhaps the most compelling evidence climate change is influencing ticks and tick-borne infections is from Canada. Prior to 1990, human infections with tick-borne pathogens were comparatively rare and limited to Powassan encephalitis, tularaemia, relapsing fever, Rocky Mountain spotted fever, and Colorado tick fever (Bouchard et al. 2019). The picture changed in the early 1990s when *I. scapularis* spread from northeastern USA into southeastern Canada; Lyme borreliosis followed and is now endemic in most Canadian provinces. Tick surveillance was introduced when it became evident the increasing incidence of Lyme borreliosis and expanding vector range in the USA threatened to spillover into Canada. The resulting surveillance data have provided a 30-year record of tick range expansion and disease emergence (Guillot et al. 2020). Other native tick species appear also to have expanded their ranges (Dergousoff et al. 2013; Gasmi et al. 2018). This northward range expansion of tick species beyond what was previously considered their geographical limits has coincided with climate warming in Canada at rates about double the magnitude of global warming. The effects of warming include relatively extreme heat, less extreme cold, longer growing seasons, and shorter periods of snow and ice cover, all of which are beneficial for tick development (Bush and Lemmen 2019). Analysis of the rate of invasion by *I. scapularis* using 20 years' surveillance data showed ticks spread faster during the warmest years irrespective of other possible determinants of tick population establishment (Leighton et al. 2012). The analysis is cited in an IPCC report as evidence rising temperatures support the emergence of vector tick populations (Cramer et al. 2014).

Similar evidence of a northward expansion has been recorded for *I. ricinus* in Scandinavia, reaching 66 °N in Sweden and 66.2 °N in Norway (Jaenson et al. 2012; Hvidsten et al. 2020). Tick abundance has increased in endemic areas, and the incidence of Lyme borreliosis and TBE in humans, and babesiosis and anaplasmosis in domesticated animals, has risen (Lindquist and Vapalahti 2008; Mysterud et al. 2017). Warming temperatures appear to be a contributing factor driving these changes though increased populations of roe deer (*Capreolus capreolus* Linnaeus, 1758) have undoubtedly played a role in supporting tick reproduction and dispersal (Jaenson et al. 2012).

Other species apparently expanding their range include *Amblyomma americanum* Linnaeus, 1758 and *Dermacentor variabilis* Say, 1821 in North America (Minigan et al. 2018; Molaei et al. 2019). Climate warming also increases the likelihood of *Rhipicephalus microplus* Canestrini, 1888, the scourge of the cattle industry, re-establishing in the USA (Giles et al. 2014). In Africa, climate change is a contributing factor in illegal cross-border movement of livestock, which in turn transports ticks into new regions (Githaka et al. 2021).

While warming temperatures are helping ticks push the physiological limits of their latitudinal ranges, they are having a similar effect on altitudinal limits. Probably the most extensive evidence has been collected in the mountainous regions of the Czech Republic where *I. ricinus* (together with TBE virus and *Borrelia burgdorferi* sensu lato) has climbed from 750 m to >1000 m above sea level, coincident with a 1.4 °C rise in mean annual air temperature over two decades (Danielová et al. 2010).

Climate change may facilitate establishment of exotic tick species in new geographical locations. Examples include *Haemaphysalis longicornis* Neumann, 1901, a native of Asia now found in the USA, and *Hyalomma marginatum marginatum* Koch, 1844, recently established in France (Stachurski and Laurence 2018; Raghavan et al. 2019b). Both species are important vectors of tick-borne pathogens, including Dabie bandavirus (formerly severe fever with thrombocytopenia virus) and *Theileria* spp. (*Ha. longicornis*), and Crimean-Congo haemorrhagic fever virus (*Hy. marginatum*). However, *Ha. longicornis* (which is parthenogenetic and bisexual) can adapt to a wide range of climate types hence other factors, such as its propensity for cattle, horses, and dogs, may play a greater role in its range expansion (Hoogstraal et al. 1968). Although *Hy. marginatum* is found in the Mediterranean region, records in France have been scarce and likely the result of immature ticks that dropped off migrating birds. This picture changed when a survey of horses in spring 2017 confirmed the presence of *Hy. marginatum* in almost all French departments with a Mediterranean coastline (Stachurski and Laurence 2018). If climate is a driving factor, establishment and range expansion of this species in France seems inevitable.

While further tick expansion is predicted in northern latitudes, a decrease in suitable areas for tick development and reproduction is expected in more southerly regions (for temperate species) though there is little evidence as yet to support this. For example, experimental comparison of survival patterns of northern and southern genotypes of *I. scapularis*, under conditions mimicking temperature and day length of northern compared with southern USA, suggests the southern limit of *I. scapularis* might retract northwards (Ginsberg et al. 2014). In Africa, retraction in the distribution of *Rhipicephalus decoloratus* Koch, 1844 appears due to displacement by the range expansion of *R. microplus*, a more heat tolerant species (Lynen et al. 2008).

Most argasid tick species are nidicolous, undergoing their entire life cycle within nests, burrows, or caves, where they have ready access to a bloodmeal. Generally, they are xerophiles, occurring in dry and hot regions (with some notable exceptions e.g. the seabird tick, *Ornithodoros maritimus* Vermeil & Marguet, 1967) (Hoogstraal 1985). Indeed, argasid ticks have among the lowest reported water loss rates of any arthropod (Dautel 1999). In Morocco, the range expansion of *Ornithodoros marocanus* Velu, 1919 (with corresponding increased incidence of relapsing fever in humans) coincides with increasing aridity in the northwest of the country (Souidi et al. 2014). However, although argasid ticks have a nearly worldwide distribution, comparatively little is known about the geographical range of most species let alone whether climate change is affecting their range. Several climatic variables have been proposed as limiting factors, such as the susceptibility of immature argasid ticks to low temperatures, and heavy rainfall, though the latter has been largely discredited (Estrada-Peña et al. 2013). While their often nidicolous lifestyle may protect argasid ticks from the inhospitable changes in climate, it may represent an achilles heel through their host dependency. For example, in Africa, *Ornithodoros moubata* Murray, 1877 live in warthog burrows where they feed exclusively on warthogs (*Phacochoerus africanus* Gmelin, 1788), especially the young which rely on their burrow for shelter (Cumming 1975). The availability of burrows is dependent on aardvark (*Orycteropus afer* Pallas, 1766) that excavate them. Recent studies suggest that climate change impacts will be particularly severe for aardvark (Rey et al. 2017). Through a somewhat circuitous route, climate change might also adversely impact warthog-dependent *O. moubata* populations and the prevalence of African swine fever virus infections (Bastos and Boinas 2021).

Increasing rates of development and reproduction

When moisture in tick habitats is nonlimiting, tick development depends primarily on warmth within a defining period to enable development of eggs, and metamorphosis of fed larvae and nymphs (Randolph 2008). For example, a relatively short summer with cool spring and autumn extend developmental times for *I. scapularis* in Canada such that one generation of its life cycle takes 3-4 years to complete compared with 2 years typically in the USA. Approximately 2800 degree days >0 °C air temperature provide the estimated minimum threshold for establishment of *I. scapularis* populations (Ogden et al. 2005). For the one-host cattle tick, *R. microplus*, the duration of the on-host phase is relatively constant (21-23 days) while the off-host phase is ~40-50 days in spring/summer and 70-120 days in autumn/winter in Brazil. Hence, off-host conditions determine the time taken to complete a generation, which may result in a remarkable 5 generations per year for *R. microplus* under higher mean temperatures and favourable humidity (Cruz et al. 2020). Though long-term empirical data on development rates from field studies are lacking, studies clearly indicate development times will reduce under climate warming if other factors (humidity, host availability, etc.) are non-limiting.

If today's climate has increased the rates of development and reproduction of ticks, the observed consequence should be an increase in tick abundance. A study of *I. ricinus* in the Tula region of Russia (eastern Europe) recorded an increased abundance of questing adult ticks over a 35-year period during which time numbers of mammalian hosts remained relatively constant while the duration of temperatures >5 °C in late summer and autumn increased (Korotkov et al. 2015). Climate-driven increases in host abundance also increase tick abundance. For example, populations of rodents (on which immature ticks feed) increase when warmer conditions result in more food (e.g. beechnuts), so-called "mast years" (Ostfeld et al. 2006; Brugger et al. 2018; Bregnard et al. 2020). For tick species that feed on livestock, climate-driven changes such as increased investment in camels and goats, which are more drought-tolerant, can change tick species diversity and abundance (Ogutu et al. 2016).

Though little is known about the impact of climate change on argasid tick development, temperature and humidity can influence the timing and rate of oviposition, as well as egg viability and female longevity. Furthermore, argasid ticks may increase production of vitellogenin in response to cold stress (Taylor and Ogihara 2021).

Phenology and seasonal activity of ticks

For most ixodid tick species, questing for a bloodmeal is triggered by environmental stimuli within their ecological niche which include photoperiod, light intensity, ambient temperature, and relative humidity (Waladde and Rice 1982; Belozerov et al. 2002). For a given location, climate warming is likely to bring forward the time when overwintered/diapausing ticks begin to quest, and/or when eggs hatch, thus changing their phenology. Records of immature *I. scapularis* feeding on small mammals, collected over a period of 19 years in New York, showed their phenology advanced by almost 3-weeks in warmer years compared with colder years (Levi et al. 2015). A 15-year study of *I. ricinus* nymphs in a temperate Swiss forest failed to detect a similar phenological change but found a strong influence of air saturation deficit, with an upper threshold reached earlier in the spring, possibly limiting the increase in questing nymph density (Hauser et al. 2018).

If climate change differentially affects the phenology of different tick stages, altering the degree of overlap in activity periods of larvae and nymphs, the consequences for many tick-borne pathogens will be profound (Gilbert 2021). This is especially true for tick-borne pathogens that induce short-term (nonsystemic) infections in their vertebrate host (e.g. TBE virus, Powassan virus, *Ehrlichia muris eauclairensis*). Such pathogens rely on cofeeding transmission between infected nymphs and uninfected larvae for their survival, i.e., maintaining the basic reproductive number, R_0, at >1. For infections that are long-lasting (usually systemic), such as *Borrelia burgdorferi* sensu stricto infections in the white-footed mouse (*Peromyscus leucopus* Rafinesque, 1818), increased asynchrony (that widens the gap between nymphal and larval activity) should increase R_0 because infected nymphs are more likely to transmit the infection to uninfected mice which then become a source of infection for larvae. Although these predictions are consistent with the prevalence of several tick-borne infections in North America, in relation to long- versus short-term infections and local synchronous/asynchronous phenology of larvae and nymphs, evidence of a climate signal of change is currently lacking (Diuk-Wasser 2021).

Tick phenotype/genotype and climate

There is some evidence different populations of the same tick species adapt their questing behaviour to different climatic conditions. Under laboratory conditions, *I. ricinus* nymphs originating from cooler climates quested at lower temperatures compared with those originating from warmer climates. Moreover, the proportion questing correlated strongly with climatic conditions from their geographical origin (Gilbert et al. 2014). Experimental studies revealed *I. scapularis* nymphs originating from northern USA are more likely to quest above ground cover while those from southern USA remain below the leaf litter (Arsnoe et al. 2015). This behavioural difference may represent adaptation to desiccation stress and helps explain the comparatively low incidence of Lyme borreliosis in southern states (Ginsberg et al. 2017; Arsnoe et al. 2019). The phenotypic difference in questing behaviour between northern and southern forms of *I. scapularis* may have a genetic basis originating from the last glacial period (Xu et al. 2020). Comparable studies for argasid tick species have not been reported although there is some evidence of adaptations to local environmental conditions in species that are geographically widespread, such as *Argas persicus* (Dusbábek 1985).

Although none of the observations of phenotypic adaptation to climatic conditions can be attributed to an impact of anthropocene climate change, they show the potential for changes in gene expression and/or adaptive evolution of tick sensory systems to play a major role in acclimatisation (Šimo et al. 2014). Furthermore, behavioural phenotypes (including altered questing and total activity levels) may be influenced by infection status, suggesting potential for interactions between infestation status, ticks, and phenotypic changes as a result of a changing climate (Herrmann and Gern 2015).

Influence of tick microbiota

Although there is no evidence climate change is affecting the microbiota of ticks, there are several observations indicating the possibility warming conditions and extreme events may have an impact. Some tick-borne pathogens are known to affect the tick phenotype in response to temperature changes. For example, *Anaplasma phagocytophilum* infection of *I. scapularis* ticks induces synthesis of tick heat shock proteins that may promote tick survival by reducing the risk of desiccation, and an 'antifreeze protein' that binds ice crystals enhancing tolerance of freezing conditions (Neelakanta et al. 2010; Busby et al. 2012). *Ixodes ricinus* nymphs infected with *B. afzelii* appear to survive desiccating conditions better than uninfected nymphs, possibly as a result of increased fat content in infected ticks (Herrmann and Gern 2010; Herrmann et al. 2013). There is also evidence some infections affect questing activity (reviewed by Herrmann and Gern, 2015; Benelli 2020). Behavioural changes that enhance host-seeking success together with greater tolerance to abiotic stress conditions will, in theory, increase the relative risk of tick-borne pathogen transmission under a warming climate. If this hypothesis is correct, the relative proportion of infected ticks on hosts should increase. Although unrelated to climate change impacts, a comparison of *B. burgdorferi* s.l. infection prevalence of female *I. ricinus* in a forest in Germany found higher prevalence in unfed ticks collected from the clothing of volunteers compared with unfed ticks collected directly from the vegetation (Faulde and Robbins 2008). Many more studies are needed to determine whether the warmer and drier conditions expected from climate change increase the relative risk of being bitten by infected ticks.

Apart from some tick-borne pathogens, little is known of the impact of raised temperatures on the tick microbiota. One study noted a change in bacterial microbiome composition with no associated tick mortality (Thapa et al. 2019). Possibly, functional redundancy in the tick microbiome ensures homeostasis under challenging environmental conditions (Estrada-Peña et al. 2020a). Hitherto, ticks harbour among the greatest diversity of heritable endosymbionts of any arthropod (Duron et al. 2017). 'Defensive' endosymbionts may help ticks adapt through their ability to protect ticks against natural enemies in new habitats as climate change promotes range expansion (Gottlieb and Duron 2021).

Future change

Predicting what may happen in the future for ticks and tick-borne infections is challenging. The diversity and complexity of the tick life cycle, the permutations of interactions in the tick vector – vertebrate host – pathogen triangle, and the often overwhelming influence of human-made changes, present a daunting picture. Added to this challenge is the effect of change on human behaviour. It can be no coincidence that exceptionally high case numbers of TBE in the Great Alpine Region of Europe were recorded in 2020, when more people than ever sought solace in nature while a pandemic raged (Rubel 2021).

At the physiological level, changes in environmental conditions are detected by the tick nervous and sensory systems. The extreme ranges of tolerance and adaptability of the tick neural/sensory system mediate behavioural plasticity, enabling remarkable adjustment to change (Šimo et al. 2014). Likewise, the tick microbiome is likely to support adaptation, with selection of endosymbiont populations that enhance tick survival (Gottlieb and Duron 2021). However, it is generally assumed ambient temperature changes do not affect tick-borne pathogen infections of ticks, in part because the extrinsic incubation period is prolonged by moulting between feeds. By contrast, numerous studies have shown temperature (and humidity) modulate the infection process of insect-borne pathogens in their vectors (Tesh et al. 1992; Carpenter et al. 2011; Hlavacova et al. 2013; Pathak et al. 2019; Turell et al. 2020). There is some evidence increasing temperature may increase the rates of development/replication of tick-borne pathogens and increase transmission risk. For example, studies on *Theileria parva*, the cause of East Coast fever in cattle, indicate transmission by infected nymphal *R. appendiculatus* incubated at either 18 or 37 °C post-engorgement, was reduced from ~72 to 24 h, respectively. The increased ambient temperature reduced the transmission processing time for the pathogen in infected ticks (Ochanda et al. 1988). For TBE virus, higher average temperatures during the summer-autumn period may be increasing the virus load in infected *I. ricinus* ticks, consequently increasing the relative risk of clinical disease in humans following an infected tick bite in warmer weather (Daniel et al. 2018).

Globally, future predictions mostly support tick population expansion rather than contraction. In Canada, warmer summers and earlier snow melt will likely support the further expansion of populations of *I. scapularis*, *Ixodes pacificus* Cooley & Kohls, 1943, *D. variabilis*, and *Dermacentor andersoni* Stiles, 1908 and the pathogens they transmit, within the constraints of habitat suitability and host availability. Other species, particularly *A. americanum* and *Ha. longicornis*, may well become established (Leighton et al. 2021). In the USA, the northern form of *I. scapularis* (and its associated pathogens) is likely to continue its range expansion until it has regained its precolonial distribution; the relative influence of climate change may then become more apparent (Fish 2021). Other species in temperate parts of the USA, e.g. *A. americanum* and *D. variabilis*, are predicted to continue their expansion northwards and to higher altitudes as temperatures increase and conditions favour tick development and questing; tick-borne pathogens (e.g. *Anaplasma marginale, Ehrlichia chaffeensis*, *Rickettsia rickettsii*) are expected to follow the expansion of their vectors (Sonenshine 2018; Raghavan et al. 2019a; Boorgula et al. 2020). Increasing temperatures are predicted to increase the chances for reintroducing *R. microplus* in major cattle-producing areas of the United States (Giles et al. 2014).

In parts of Europe where humidity is not a constraint, further expansion in tick populations is considered inevitable, particularly for *I. ricinus* and *Dermacentor reticulatus* Fabricius, 1794, with consequential medical and veterinary impacts (Gilbert et al. 2014; Alkishe et al. 2017; Zając 2021). When new tick populations establish in sparsely populated regions, the impact on human health may be minimal; however, when new species are introduced, e.g. *Ixodes persulcatus* Schulze, 1930 in Sweden, new pathogens may follow e.g. Siberian and Far Eastern subtypes of TBE virus which cause more severe disease than the European subtype (Jaenson et al. 2016; Kjær et al. 2019). In Russia, socioeconomic factors that give rise to sharp increases in the frequency of human contact with ticks (*I. ricinus* and *I. persulcatus*), are considered more likely future drivers of increased morbidity levels in TBE and Lyme borreliosis compared with climate change (Korenberg 2021).

In southern France and other Mediterranean regions of Europe, *Hy. marginatum* is expected to become permanently established, bringing with it the threat of Crimean-Congo haemorrhagic fever (CCHF), a severe disease in humans (Stachurski et al. 2021). However, in Turkey, the epicentre of CCHF, populations of *Hy. marginatum* are predicted to decline as livestock management practices adapt to climate change and other pressures, and become less supportive of this 2-host tick (Kar and Gargili Keles 2021).

One route for introducing new tick species is via dispersal by birds, particularly during bird migrations (Hoogstraal et al. 1961, 1963; de la Fuente et al. 2015; Coughlan et al. 2017; Estrada-Peña et al. 2020b). Climate change appears to be affecting the numbers of migrating birds and their migration patterns (Fiedler et al. 2006; Visser et al. 2009; Bairlein 2016). For the Western Palaearctic, this implies a partial reduction in long-distance dispersal from Afro-Tropical regions and a potential increase in transportation of ticks from the Mediterranean basin and adjacent regions. Besides reducing long-dispersal, a patchy tick distribution may develop as engorged ticks drop off along migration routes giving rise to 'stepping stone' changes in the ixodid tick fauna (Kelly et al. 2021). Permanent establishment of *Hy. rufipes* in Europe and Turkey, facilitated by long- and short-distance dispersal by birds, would be a major change to the resident ixodid tick fauna.

While models predict the northward range expansion of several important ixodid tick species, it is less clear what will happen at the southern limit of their range. For example, in the case of *I. ricinus* in the Mediterranean region, where lack of humidity (rather than low temperature) impacts survival, ecosystem niche models have a high level of uncertainty (Alkishe et al. 2017). However, spatial distributions models of *I. ricinus*, and a climate envelope model for Lyme borreliosis at 2 °C of global warming, predict a retraction in the range of the vector and reduced disease incidence in southern and central Europe (Cox et al. 2021; Wint and Alexander, 2021). Models restricted to climatically analogous areas estimate a reduction in areas of Brazil suitable for *Amblyomma cajennense* s.s. Fabricius, 1787 and *Amblyomma sculptum* Berlese, 1888 (Oliveira et al. 2017). In a global assessment of the potential future distribution of *Rhipicephalus sanguineus* sensu lato, losses in suitable habitats were identified in South America, eastern USA, and southern Europe; most of the uncertainty in the ecological niche models was due to variation from replicates in model projections (Alkishe et al. 2020).

Predictions of future effects of climate change on argasid ticks and associated diseases are few. Since most argasids have a sheltered, nidicolous life-style, they may be more susceptible to indirect impacts. As already mentioned, the future of *O. moubata* in some parts of Africa is dependent on the uncertain future of aardvark. A significant challenge for modelling is the paucity of accurate occurrence data (Vial et al. 2018). One possible exception is *Ornithodoros hermsi* Wheeler, Herms & Meyer, 1935, the vector of the relapsing fever spirochaete, *Borrelia hermsii*, in western North America. Using maximum entropy species distribution modelling, this vector is projected to move to higher altitudes while maintaining its current geographical range (Sage et al. 2017).

A common framework for predicting the future of ticks and tick-borne infections has not been established. Factors to consider in building such a framework include climate, land use, vegetation, and vertebrate host populations, besides tick physiology, stress, mortality, fecundity, and activity (Estrada-Peña et al. 2021). However, there are many gaps in our understanding of what determines the distribution and activity of many important tick species, let alone the incidence and prevalence of tick-borne infections. Added to these limitations are the changes in human behaviour, land use, and livestock and wildlife management, in response to rapid climate change. The challenge in predicting the future is illustrated by the unrealised prediction that TBE virus infections would no longer pose a threat to human health in France, Switzerland, Croatia, and much of Austria in the 2020s (Randolph and Rogers 2000). Indeed, as the pace of change increases, extant data become less directly applicable to the future. In countries where tick-borne infections of livestock affect peoples' livelihoods, a One Health approach is advocated. Generally, solutions are needed that are local and bespoke, and can be aided by scenario-based models to inform monitoring and intervention strategies (Rocklöv and Dubrow 2020).

Declarations

Conflicts of interest The author has no conflicts of interest to declare relevant to the content of this article.

References

Alkishe A, Cobos ME, Peterson AT, Samy AM (2020) Recognizing sources of uncertainty in disease vector ecological niche models: An example with the tick *Rhipicephalus sanguineus* sensu lato. PECON 18:91–102. https://doi.org/10.1016/j.pecon.2020.03.002

Alkishe AA, Peterson AT, Samy AM (2017) Climate change influences on the potential geographic distribution of the disease vector tick *Ixodes ricinus*. PLoS One 12:e0189092. https://doi.org/10.1371/journal.pone.0189092

Allen M, de Coninck H, Dube OP et al (2018) Technical Summary: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat. https://www.ipcc.ch/site/assets/uploads/sites/2/2018/12/SR15_TS_High_Res.pdf

Apanaskevich DA, Oliver JH (2014) Life cycles and natural history of ticks. In: Sonenshine DE, Roe RM (eds) Biology of Ticks, 2nd edn. Oxford University Press, New York, pp 59–73

Arsnoe IM, Hickling G, Ginsberg H et al (2015) Different populations of blacklegged tick nymphs exhibit differences in questing behavior that have implications for human Lyme disease risk. PLoS One 10:e0127450. https://doi.org/10.1371/journal.pone.0127450

Arsnoe I, Tsao JI, Hickling GJ (2019) Nymphal *Ixodes scapularis* questing behavior explains geographic variation in Lyme borreliosis risk in the eastern United States. Ticks Tick Borne Dis 10:553–563. https://doi.org/10.1016/j.ttbdis.2019.01.001

Bairlein F (2016) Migratory birds under threat. Science 354:547–548. https://doi.org/10.1126/science.aah6647

Bastos A, Boinas F (2021) *Ornithodoros* tick vectors and African swine fever virus. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 405–412. https://doi.org/10.1079/9781789249637

Bellouin N, Quaas J, Gryspeerdt E et al (2019) Bounding global aerosols radiative forcing of climate change. ROG 58:e2019RG000660. https://doi.org/10.1029/2019RG000660

Belozerov VN, Fourie LJ, Kok DJ (2002) Photoperiodic control of developmental diapause in nymphs of prostriate ixodid ticks (Acari: Ixodidae). Exp Appl Acarol 28:163–168. https://doi.org/10.1023/A:1025377829119

Benelli G (2020) Pathogens manipulating tick behavior – through a glass, darkly. Pathogens 9:664. https://doi.org/10.3390/pathogens9080664

Boorgula GDY, Peterson T, Foley D et al (2020) Assessing the current and future potential geographic distribution of the American dog tick, *Dermacentor variabilis* (Say) (Acari: Ixodidae) in North America. PLoS One 15:e0237191. https://doi.org/10.1371/journal.pone.0237191

Bouchard C, Dibernardo A, Koffi J et al (2019) Increased risk of tick-borne diseases with climate and environmental changes. Can Commun Dis Rep 45:83–89. https://doi.org/10.14745/ccdr.v45i04a02

Bregnard C, Rais O, Voordouw MJ (2020) Climate and tree seed production predict the abundance of the European Lyme disease vector over a 15-year period. Parasite Vector 13:408. https://doi.org/10.1186/s13071-020-04291-z

Brugger K, Walter M, Chitimia-Dobler L et al (2018) Forecasting next season's *Ixodes ricinus* nymphal density: the example of southern Germany 2018. Exp Appl Acarol 75:281–288. https://doi.org/10.1007/s10493-018-0267-6

Busby AT, Ayllón N, Kocan K et al (2012) Expression of heat shock proteins and subolesin affects stress responses, *Anaplasma phagocytophilum* infection and questing behaviour in the tick, *Ixodes scapularis*. Med Vet Entomol 26:92–102. https://doi.org/10.1111/j.1365-2915.2011.00973.x

Bush E, Lemmen DS (eds) (2019) Canada's changing climate report. Government of Canada, Ottawa, 444 pp. https://changingclimate.ca/CCCR2019/

Carpenter S et al (2011) Temperature dependence of the extrinsic incubation period of orbiviruses in *Culicoides* biting midges. PLoS One 6:e27987. https://doi.org/10.1371/journal.pone.0027987

Černý J, Elsterová J, Culler L (2021) Melting, melting pot - climate change and its impact on ticks and tick-borne pathogens in the Arctic. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 460–468. https://doi.org/10.1079/9781789249637

Coughlan NE, Kelly T, Davenport J, Jansen MAK (2017) Up, up and away: bird-mediated ectozoochorous dispersal between aquatic environments. Freshw Biol 62:631–648. https://doi.org/10.1111/fwb.12894

Cox P, Huntingford C, Sparey M, Nuttall P (2021) Climate change and Lyme disease. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, Oxon, UK, pp 18–25. https://doi.org/10.1079/9781789249637

Cramer W, Yohe G, Auffhammer M et al (2014) Detection and attribution of observed impacts. In: Field C, Barros V, Dokken D et al (eds) Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and Sectoral Aspects Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, pp 979–1037

Cruz BC, Mendes AFdeL, Maciel WG et al (2020) Biological parameters for *Rhipicephalus microplus* in the field and laboratory and estimation of its annual number of generations in a tropical region. Parasitol Res 119:2421–2430. https://doi.org/10.1007/s00436-020-06758-5

Cumming DHM (1975) A field study of the ecology and behaviour of Warthog. Museum Memoir 7, Nat Mus Mon Rhodesia, Salisbury

Daniel M, Danielová V, Fialová A et al (2018) Increased relative risk of tick-borne encephalitis in warmer weather. Front Cell Infect Microbiol 8:90. https://doi.org/10.3389/fcimb.2018.00090

Danielová V, Daniel M, Schwarzová L et al (2010) Integration of a tick-borne encephalitis virus and *Borrelia burgdorferi* sensu lato into mountain ecosystems, following a shift in the altitudinal limit of distribution of their vector, *Ixodes ricinus* (Krkonoše Mountains, Czech Republic). Vector Borne Zoonotic Dis 10:223–230. https://doi.org/10.1089/vbz.2009.0020

Dautel H (1999) Water loss and metabolic water in starving *Argas reflexus* nymphs (Acari: Argasidae). J Insect Physiol 45:55–63. https://doi.org/10.1016/S0022-1910(98)00099-7

de la Fuente J, Estrada-Peña A, Cabezas-Cruz A, Brey R (2015) Flying ticks: anciently evolved associations that constitute a risk of infectious disease spread. Parasite Vector 8:538. https://doi.org/10.1186/s13071-015-1154-1

Dergousoff SJ, Galloway T, Lindsay L et al (2013) Range expansion of *Dermacentor variabilis* and *Dermacentor andersoni* (Acari: Ixodidae) near their northern distributional limits. J Med Entomol 50:510–520. https://doi.org/10.1603/ME12193

Diuk-Wasser M (2021) It's all in the timing: effect of tick phenology on pathogen transmission dynamics. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, Oxon, UK, pp 283–292. https://doi.org/10.1079/9781789249637

Duron O, Binetruy F, Noël V et al (2017) Evolutionary changes in symbiont community structure in ticks. Mol Ecol 26:2905–2921. https://doi.org/10.1111/mec.14094

Dusbábek F (1985) Biological comparison of different populations of *Argas* (*Persicargas*) *persicus* (Oken). Folia Parasit 32:255–263

Estrada-Peña A, Gray J, Kahl O et al (2013) Research on the ecology of ticks and tick-borne pathogens - methodological principles and caveats. Front Cell Infect Microbiol 3:29. https://doi.org/10.3389/fcimb.2013.00029

Estrada-Peña A, Cabezas-Cruz A, Obregón D (2020a) Behind taxonomic variability: the functional redundancy in the tick microbiome. Microorg 8:1829. https://doi.org/10.3390/microorganisms8111829

Estrada-Peña A, D'Amico G, Fernández-Ruiz N (2020b) Modelling the potential spread of *Hyalomma marginatum* ticks in Europe by migratory birds. Int J Parasitol 51:1–11. https://doi.org/10.1016/j.ijpara.2020.08.004

Estrada-Peña A, Fernández-Ruiz N, de la Fuente J (2021) Climate, ticks, and pathogens: gaps and caveats. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 240–246. https://doi.org/10.1079/9781789249637

Faulde MK, Robbins RG (2008) Tick infestation risk and *Borrelia burgdorferi* s.l. infection-induced increase in host-finding efficacy of female *Ixodes ricinus* under natural conditions. Exp Appl Acarol 44:137. https://doi.org/10.1007/s10493-008-9131-4

Fiedler W, Bairlein F, Köppen U (2006) Using large-scale data from ringed birds for the investigation of climate change on migrating birds: pitfalls and prospects. In: Moller AP, Fiedler A, Berthold P (eds) Birds and Climate Change. Academic, London, pp 49–67

Fish D (2021) Range expansion of *Ixodes scapularis* in the USA. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 176–182. https://doi.org/10.1079/9781789249637

Gasmi S, Bouchard C, Ogden N et al (2018) Evidence for increasing densities and geographic ranges of tick species of public health significance other than *Ixodes scapularis* in Québec, Canada. PLoS One 13:e0201924. https://doi.org/10.1371/journal.pone.0201924

Gilbert L (2021) The impacts of climate change on ticks and tick-borne disease risk. Annu Rev Entomol 66:273–288. https://doi.org/10.1146/annurev-ento-052720-094533

Gilbert L, Aungier J, Tomkins JL (2014) Climate of origin affects tick (*Ixodes ricinus*) host-seeking behavior in response to temperature: implications for resilience to climate change? Ecol Evol 4:1186–1198. https://doi.org/10.1002/ece3.1014

Giles JR, Peterson A, Busch J et al (2014) Invasive potential of cattle fever ticks in the southern United States. Parasite Vector 7:189. https://doi.org/10.1186/1756-3305-7-189

Ginsberg HS, Rulison E, Acevedo A et al (2014) Comparison of survival patterns of northern and southern genotypes of the North American tick *Ixodes scapularis* (Acari: Ixodidae) under northern and southern conditions. Parasite Vector 7:394. https://doi.org/10.1186/1756-3305-7-394

Ginsberg HS, Albert M, Acevedo A et al (2017) Environmental factors affecting survival of immature *Ixodes scapularis* and implications for geographical distribution of Lyme disease: the climate/behavior hypothesis. PLoS One 12:1–17. https://doi.org/10.1371/journal.pone.0168723

Githaka N, Kanduma E, Bishop R (2021) Role of climate and other factors in determining the dynamics of tick and tick-transmitted pathogen populations and distribution in western, central, and eastern Africa. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 486–491. https://doi.org/10.1079/9781789249637

Gottlieb Y, Duron O (2021) Expected transitions in ticks and their heritable endosymbionts under environmental changes. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 61–66. https://doi.org/10.1079/9781789249637

Guillot C, Badcock J, Clow K et al (2020) Sentinel surveillance of Lyme disease risk in Canada, 2019: results from the first year of the Canadian Lyme Sentinel Network (CaLSeN). Can Commun Dis Rep 46:354–361. https://doi.org/10.14745/ccdr.v46i10a08

Hauser G, Rais O, Cadenas FM et al (2018) Influence of climatic factors on *Ixodes ricinus* nymph abundance and phenology over a long-term monthly observation in Switzerland (2000–2014). Parasite Vector 11:289. https://doi.org/10.1186/s13071-018-2876-7

Herrmann C, Gern L (2010) Survival of *Ixodes ricinus* (Acari: Ixodidae) under challenging conditions of temperature and humidity is influenced by *Borrelia burgdorferi* sensu lato infection. J Med Entomol 47:1196–1204. https://doi.org/10.1603/ME10111

Herrmann C, Gern L (2015) Search for blood or water is influenced by *Borrelia burgdorferi* in *Ixodes ricinus*. Parasite Vector 8:6. https://doi.org/10.1186/s13071-014-0526-2

Herrmann C, Voordouw MJ, Gern L (2013) *Ixodes ricinus* ticks infected with the causative agent of Lyme disease, Borrelia burgdorferi sensu lato, have higher energy reserves. Int J Parasitol 43:477–483. https://doi.org/10.1016/j.ijpara.2012.12.010

Hlavacova J, Votypka J, Volf P (2013) The effect of temperature on *Leishmania* (Kinetoplastida: Trypanosomatidae) development in sand flies. J Med Entomol 50:955–958. https://doi.org/10.1603/ME13053

Hoen AG, Margos G, Bent SJ et al (2009) Phylogeography of *Borrelia burgdorferi* in the eastern United States reflects multiple independent Lyme disease emergence events. PNAS 106:15013–15018. https://doi.org/10.1073/pnas.0903810106

Hoogstraal H, Kaiser M, Taylor M et al (1961) Ticks (Ixodoidea) on birds migrating from Africa to Europe and Asia. Bull WHO 24:197–212

Hoogstraal H, Kaiser M, Taylor M et al (1963) Ticks (Ixodoidea) on birds migrating from Europe and Asia to Africa. Bull WHO 28:235–262

Hoogstraal H, Roberts F, Kohls G, Tipton VJ (1968) Review of *Haemaphysalis* (Kaiseriana) *longicornis* Neumann (Resurrected) of Australia, New Zealand, New Caledonia, Fiji, Japan, Korea, and Northeastern China and USSR, and its parthenogenetic and bisexual populations (Ixodoidea, Ixodidae). J Parasitol 54:1197–1213. http://www.ajtmh.org/content/journals/, https://doi.org/10.4269/ajtmh.16-0967

Hoogstraal H (1985) Argasid and Nuttalliellid ticks as parasites and vectors. Adv Parasitol 24:135–238. https://doi.org/10.1016/S0065-308X(08)60563-1

Hvidsten D, Frafjord K, Gray JS et al (2020) The distribution limit of the common tick, *Ixodes ricinus*, and some associated pathogens in north-western Europe. Ticks Tick Borne Dis 11:101388. https://doi.org/10.1016/j.ttbdis.2020.101388

Jaenson TGT, Jaenson D, Eisen L et al (2012) Changes in the geographical distribution and abundance of the tick *Ixodes ricinus* during the past 30 years in Sweden. Parasite Vector 5:1–15. https://doi.org/10.1186/1756-3305-5-8

Jaenson TGT, Värv K, Fröjdman I et al (2016) First evidence of established populations of the taiga tick *Ixodes persulcatus* (Acari: Ixodidae) in Sweden. Parasite Vector 9:377. https://doi.org/10.1186/s13071-016-1658-3

Kar S, Gargili Keles A (2021) Possible direct and human-mediated impact of climate change on tick populations in Turkey. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 115–124. https://doi.org/10.1079/9781789249637

Kelly TC, Healy JE, Coughlan NE (2021) Birds, ticks, and climate change. In: Nuttall PA (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 96–109. https://doi.org/10.1079/9781789249637

Kjær LJ, Soleng A, Edgar K et al (2019) Predicting and mapping human risk of exposure to *Ixodes ricinus* nymphs using climatic and environmental data. Denmark Norway Sweden 2016 Euro Surveill 24:1–11. https://doi.org/10.2807/1560-7917.ES.2019.24.9.1800101

Knulle W, Rudolph D (1982) Humidity relationships and water balance of ticks. In: Obenchain F, Galun R (eds) Physiology of Ticks. Pergamon Press, Oxford, pp 43–70

Korenberg E (2021) Impact of climate change on ticks and tick-borne infections in Russia. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 438–443. https://doi.org/10.1079/9781789249637

Korenberg EI (2009) Recent epidemiology of tick-borne encephalitis: an effect of climate change? Adv Virus Res 74:123–144. https://doi.org/10.1016/S0065-3527(09)74004-7

Korotkov Y, Kozlova T, Kozlovskaya L (2015) Observations on changes in abundance of questing *Ixodes ricinus*, castor bean tick, over a 35-year period in the eastern part of its range (Russia, Tula region). Med Vet Entomol 29:129–136. https://doi.org/10.1111/mve.12101

Leighton PA, Koffi J, Pecat Y et al (2012) Predicting the speed of tick invasion: an empirical model of range expansion for the Lyme disease vector *Ixodes scapularis* in Canada. J Appl Ecol 49:457–464. https://doi.org/10.1111/j.1365-2664.2012.02112.x

Leighton PA, Lindsay LR, Ogden NH (2021) Climate and the emergence of tick-borne disease in Canada. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 507–512. https://doi.org/10.1079/9781789249637

Levi T, Keesing F, Oggenfuss K, Ostfeld RS (2015) Accelerated phenology of blacklegged ticks under climate warming. Phil Trans Roy Soc B 370:20130556. https://doi.org/10.1098/rstb.2013.0556

Lindquist L, Vapalahti O (2008) Tick-borne encephalitis. Lancet 371:1861–1871. https://doi.org/10.1684/mtp.2015.0566

Lynen G, Zeman P, Bakuname C et al (2008) Shifts in the distributional ranges of *Boophilus* ticks in Tanzania: evidence that a parapatric boundary between *Boophilus microplus* and *B. decoloratus* follows climate gradients. Exp Appl Acarol 44:147–164. https://doi.org/10.1007/s10493-008-9134-1

Minigan JN, Hager H, Peregrine A, Newman JA (2018) Current and potential future distribution of the American dog tick (*Dermacentor variabilis*, Say) in North America. Ticks Tick Borne Dis 9:354–362. https://doi.org/10.1016/j.ttbdis.2017.11.012

Molaei G, Little E, Williams S, Stafford KC (2019) Bracing for the worst — range expansion of the Lone Star tick in the northeastern United States. NEJM 381:2189–2192. https://doi.org/10.1056/NEJMp1911661

Myhre G, Shindell D, Pongratz J (2014) Anthropogenic and natural radiative forcing. In: Intergovernmental Panel on Climate Change (ed.) Climate Change 2013 – The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press, pp 659–740. https://doi.org/10.1017/CBO9781107415324.018

Mysterud A, Jore S, Østerås O, Viljugrein H (2017) Emergence of tick-borne diseases at northern latitudes in Europe: a comparative approach. Sci Rep 7:16316. https://doi.org/10.1038/s41598-017-15742-6

Neelakant G, Sultana H, Fish D et al (2010) *Anaplasma phagocytophilum* induces *Ixodes scapularis* ticks to express an antifreeze glycoprotein gene that enhances their survival in the cold. J Clin Invest 120:3179–3190. https://doi.org/10.1172/JCI42868

Nuttall P (ed) (2021) Climate, Ticks and Disease. CABI, Wallingford, 552 pp. https://doi.org/10.1079/9781789249637

Ochanda H, Young A, Mutugi J et al (1988) The effect of temperature on the rate of transmission of *Theileria parva* infection to cattle by its tick vector, *Rhipicephalus appendiculatus*. Parasitology 97:239–245. https://doi.org/10.1017/S0031182000058443

Ogden NH, Bigras-Poulin M, O'Callaghan CJ, et al (2005) A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. Int J Parasitol 35:375–389. https://doi.org/10.1016/j.ijpara.2004.12.013

Ogutu JO, Piepho H, Said M et al (2016) Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: what are the causes? PLoS One 11:e0163249. https://doi.org/10.1371/journal.pone.0163249

Oliveira SVd, Romero-Alvarez D, Martins TF et al (2017) *Amblyomma* ticks and future climate: range contraction due to climate warming. Acta Trop 176:340–348. https://doi.org/10.1016/j.actatropica.2017.07.033

Ostfeld RS, Canham C, Oggenfuss K et al (2006) Climate, deer, rodents, and acorns as determinants of variation in Lyme disease risk. PLoS Biol 4:e145. https://doi.org/10.1371/journal.pbio.0040145

Pathak AK, Shiau J, Thomas M et al (2019) Field relevant variation in ambient temperature modifies density-dependent establishment of *Plasmodium falciparum* gametocytes in mosquitoes. Front Microbiol 10: 2651. https://www.frontiersin.org/article/, https://doi.org/10.3389/fmicb.2019.02651

Raghavan RK, Peterson A, Cobos ME et al (2019a) Current and future distribution of the Lone Star tick, *Amblyomma americanum* (L.) (Acari: Ixodidae) in North America. PLoS One 14:e0209082. https://doi.org/10.1371/journal.pone.0209082

Raghavan RK, Barker S, Cobos ME et al (2019b) Potential spatial sistribution of the newly introduced Long-horned tick, *Haemaphysalis longicornis* in North America. Sci Rep 9:1–8. https://doi.org/10.1038/s41598-018-37205-2

Randolph SE (2008) The impact of tick ecology on pathogen transmission dynamics. In: Bowman AS, Nuttall PA (eds) Ticks: Biology, Disease and Control. Cambridge University Press, Cambridge, pp 40–72

Randolph SE, Rogers DJ (2000) Fragile transmission cycles of tick-borne encephalitis virus may be disrupted by predicted climate change. Proc Roy Soc B 267:1741–1744. https://doi.org/10.1098/rspb.2000.1204

Rey B, Fuller A, Mitchell D et al (2017) Drought-induced starvation of aardvarks in the Kalahari: an indirect effect of climate change. Biol Lett 13:20170301. https://doi.org/10.1098/rsbl.2017.0301

Rocklöv J, Dubrow R (2020) Climate change: an enduring challenge for vector-borne disease prevention and control. Nature Immunol 21:479–483. https://doi.org/10.1038/s41590-020-0648-y

Rubel F (2021) Climate change and tick-borne encephalitis in the Greater Alpine Region. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 354–359. https://doi.org/10.1079/9781789249637

Sage KM, Johnson T, Teglas M et al (2017) Ecological niche modeling and distribution of *Ornithodoros hermsi* associated with tick-borne relapsing fever in western North America. PLoS Negl Trop Dis 11:e0006047. https://doi.org/10.1371/journal.pntd.0006047

Šimo L, Sonenshine DE, Park Y, Žitnan D (2014) The nervous and sensory systems: structure, function, proteomics and genomics. In: Sonenshine DE, Roe RM (eds) Biology of Ticks Volume 1, 2nd edn. Oxford University Press, New York, pp 309–367

Sonenshine DE (2018) Range expansion of tick disease vectors in North America: implications for spread of tick-borne disease. Int J Environ Res Public Health 15:478. https://doi.org/10.3390/ijerph15030478

Souidi Y, Boudebouch N, Ezikouri S et al (2014) *Borrelia crocidurae* in *Ornithodoros* ticks from northwestern Morocco: a range extension in relation to climatic change? J Vector Ecol 39:316–320. https://doi.org/10.1111/jvec.12106

Stachurski F et al (2021) Climate change alone cannot explain altered tick distribution across Europe: a spotlight on endemic and invasive tick species. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 125–131. https://doi.org/10.1079/9781789249637

Stachurski F, Laurence V (2018) Installation de la tique *Hyalomma marginatum*, vectrice du virus de la fièvre hémorragique de Crimée-Congo, en France continentale. Bull Epidémiol 84:37–41

Taylor D, Ogihara M (2021) Climate influences on reproduction and immunity in the soft tick, *Ornithodoros moubata*. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 74–83. https://doi.org/10.1079/9781789249637

Tesh TB, Lubroth J, Guzman H (1992) Simulation of arbovirus overwintering: survival of Toscana virus (Bunyaviridae: Phlebovirus) in its natural sand fly vector *Phlebotomus perniciosus*. Am J Trop Med Hyg 47:574–581

Thapa S, Zhang Y, Allen MS (2019) Effects of temperature on bacterial microbiome composition in *Ixodes scapularis* ticks. MicrobiologyOpen 8:e00719. https://doi.org/10.1002/mbo3.719

Turell MJ, Cohnstaedt LW, Wilson WC (2020) Effect of environmental temperature on the ability of *Culex tarsalis* and *Aedes taeniorhynchus* (Diptera: Culicidae) to transmit Rift Valley fever virus. Vector Borne Zoonotic Dis 20:454–460. https://doi.org/10.1089/vbz.2019.2554

Vial L, Ducheyne E, Filatov S et al (2018) Spatial multi-criteria decision analysis for modelling suitable habitats of *Ornithodoros* soft ticks in the Western Palearctic region. Vet Parasitol 249:2–16. https://doi.org/10.1016/j.vetpar.2017.10.022

Visser ME, Perdeck AC, Van Balen JH, Both C (2009) Climate change leads to decreasing bird migration distances. Glob Change Biol 15:1859–1865. https://doi.org/10.1111/j.1365-2486.2009.01865.x

Waladde SM, Rice MJ (1982) The sensory basis of tick feeding behaviour. In: Obenchain FD, Galun R (eds) Physiology of Ticks. Pergamon Press, Oxford, pp 71–118

Wint W, Alexander N (2021) Challenges of modelling and projecting tick distributions. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 32–37. https://doi.org/10.1079/9781789249637

WMO (2020) Reported new record temperature of 38°C north of Arctic Circle [Online]. https://public.wmo.int/en/media/news/reported-new-record-temperature-of-38 %C2 %B0c-north-of-arctic-circle. Accessed 22/06/21

Xu G, Wielstra B, Rich SM (2020) Northern and southern blacklegged (deer) ticks are genetically distinct with different histories and Lyme spirochete infection rates. Sci Rep 10:1–9. https://doi.org/10.1038/s41598-020-67259-0

Zając Z (2021) Climate impacts on *Dermacentor reticulatus* tick population dynamics and range. In: Nuttall P (ed) Climate, Ticks and Disease. CABI, Wallingford, pp 166–170. https://doi.org/10.1079/9781789249637