



Climate change impacts on ticks and tick-borne infections

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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 two-fold 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 (Knülle 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 maroccanus* 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 $>0^{\circ}\text{C}$ 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 $>5^{\circ}\text{C}$ 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; Belozarov 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 euclairensis*). 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; Arnsnoe 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.

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