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## Changing distributions of ticks: causes and consequences

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**Abstract** Today, we are witnessing changes in the spatial distribution and abundance of many species, including ticks and their associated pathogens. Evidence that these changes are primarily due to climate change, habitat modifications, and the globalisation of human activities are accumulating. Changes in the distribution of ticks and their invasion into new regions can have numerous consequences including modifications in their ecological characteristics and those of endemic species, impacts on the dynamics of local host populations and the emergence of human and livestock disease. Here, we review the principal causes for distributional shifts in tick populations and their consequences in terms of the ecological attributes of the species in question (i.e. phenotypic and genetic responses), pathogen transmission and disease epidemiology. We also describe different methodological approaches currently used to assess and predict such changes and their consequences. We finish with a discussion of new research avenues to develop in order to improve our understanding of these host–vector–pathogen interactions in the context of a changing world.

**Keywords** Global change · Habitat modification · Ixodidae · Argasidae · Tick-borne disease

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## Introduction

Today, we are witnessing major changes across the planet. Changes in landscape (land use and land cover), vegetation, and climate coincide with changes in human habitations and settlement patterns, modern agricultural and social activities, increases in international trade, population growth, wide-scale movements of humans and livestock and increases in environmental pollution (Walker and Steffen 1999; Fayer 2000; Sutherst 2001; Biello 2011). For example, an overall increase in world-wide mean temperatures of 0.10–0.16 °C per decade was reported for the second half of the twentieth century, and temperature is expected to increase significantly in the next 100 years (IPCC 2007). Such temperature changes will have long-term impacts on ecosystems and thus, on the plant and animal species they contain (IPCC 2002; Parmesan and Yohe 2003; Robinson et al. 2003; Thuiller et al. 2006; Fries and Mayer 2009). Faced with environmental change, living organisms have three options: adapt to the new conditions, move to a more appropriate habitat (Chown et al. 2010), or do nothing and go extinct. In some cases, populations respond via modifications in their life history traits (by selection or plasticity). For instance, shifts in breeding phenology have been demonstrated in some bird species (McCarty 2001; Root et al. 2006); the timing of spring migration occurs earlier, which in turn advances the breeding period (i.e. egg-laying, hatching and fledgling) so that the peak in food availability coincides with the most energy-demanding period of reproduction (Butler 2003; Leech and Crick 2007; Matthysen et al. 2011). Similar patterns have also been observed in amphibians, where adults emerge from hibernation and spawn earlier in the spring (Blaustein et al. 2001; Walther et al. 2002). However, when life history traits are inflexible, due to a lack of standing genetic variation or phenotypic plasticity, changes in habitat suitability can mean the local extinction of a species and result in a shift in its distribution.

A vast component of global biodiversity is made up of parasitic organisms (e.g. de Meeûs and Renaud 2002). In the context of a changing world, situations that were formerly unfit for a parasite, due to environmental constraints or host availability, can become favourable (Estrada-Peña 2001; Estrada-Peña and Venzal 2006; Cumming and Van Vuuren 2006). Global change can therefore lead to the emergence or re-emergence of infectious and parasitic diseases (Daily and Ehrlich 1996; Fayer 2000; Patz et al. 2000; Polley 2005; Wilcox and Gubler 2005). In the same way, some environments may become sub-optimal for parasites, leading to the disappearance of certain diseases or their confinement to small areas (Randolph and Rogers 2000; Rogers and Randolph 2006). For example, this is likely the case for malaria in Africa, where it has been suggested that climate change may result in a range contraction of the disease over the next decades (Thomas et al. 2004; Gething et al. 2010).

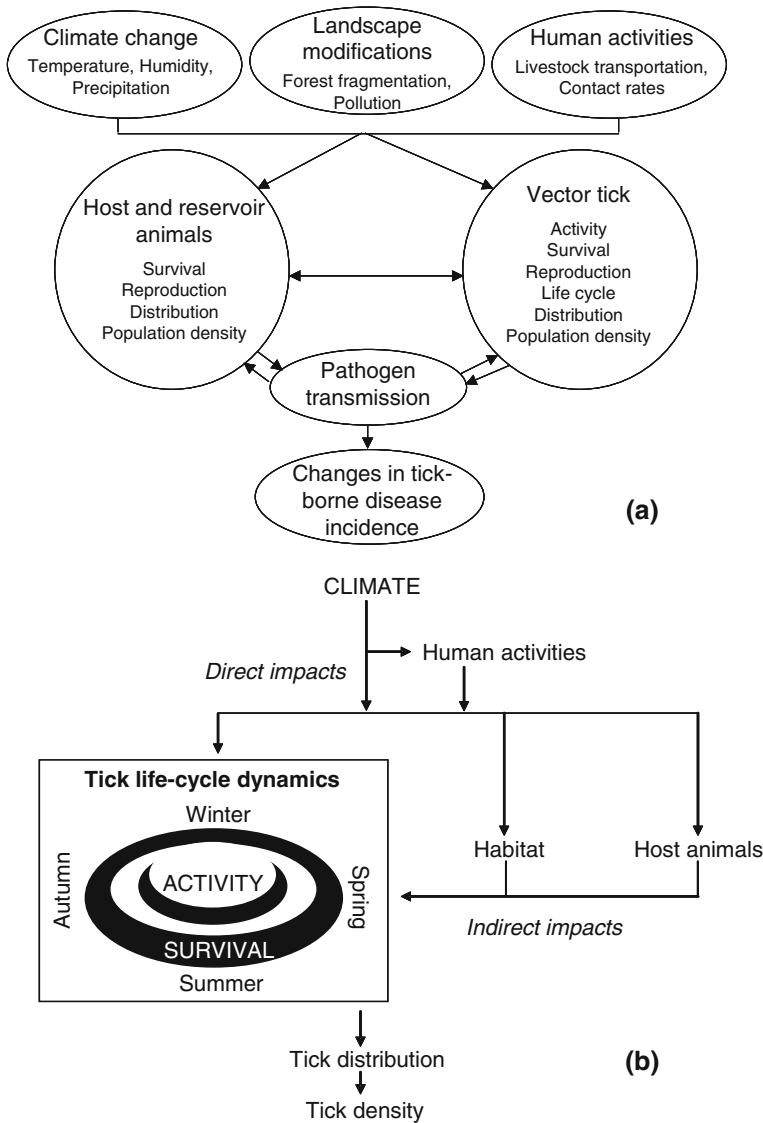
Among parasites, ticks are particularly interesting to consider from the perspective of climate change due to the strong dependence on both biotic and abiotic conditions for their local survival and reproduction. Ticks are often only associated with their hosts for the period of the bloodmeal, during which time they undergo specific and intense interactions at the host interface (i.e. physiological and immunological defences). The local presence of ticks therefore depends on the presence and abundance of appropriate hosts (Gilot and Perez-Eid 1998; Gray 1998). As ticks have only limited independent dispersal abilities (Falco and Fish 1991), patterns of colonisation will depend on the large-scale movements of the hosts. However, the simple arrival in new environment is not enough in and of itself. During the free-living phase of their life cycle, ticks are very vulnerable to environmental conditions, often requiring very specific conditions of humidity and temperature (Gray 1991; Vassallo et al. 2000; Estrada-Peña et al. 2004). Indeed, it has been postulated that

tick distributions are more limited by climatic conditions than by the presence and abundance of specific host types (Klompen et al. 1996; Cumming 2002). Finally, ticks are vectors of a wide-range of human and livestock disease agents. In this way, the factors that limit their distribution are essential for understanding and predicting disease occurrence and emergence.

How have tick distributions changed and what are the consequences of these changes? In this review, we will explore these questions by synthesizing what is currently known about the distributional changes of various tick species and their presumed causes. We will also discuss the consequences of these changes in terms of the ecology and evolution of tick-host interactions and the circulation of tick-borne disease. We will provide a brief overview of the methods used by scientists to predict, detect and understand the changing distribution of hosts, vectors and pathogens. We will then illustrate these aspects using several case studies where the invasion of ticks into new regions has had (or may have) major impacts on the local fauna and the transmission of human and livestock pathogens. Finally, we will discuss future research required to better understand the impacts of global change on host-ectoparasite interactions and vector-borne disease.

### Distributional changes in ticks and their causes

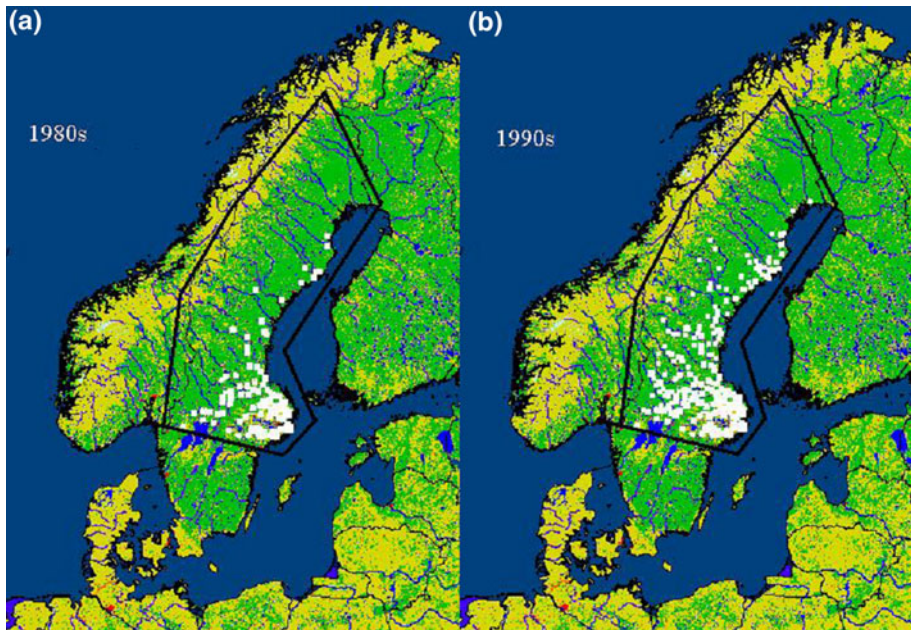
Ticks, and the pathogens they transmit, have been significant health burdens throughout the world for many centuries and, over this time period, their ranges have expanded, contracted, and shifted. Over the last 30 years, there has been a steady increase in the abundance and spatial distribution of many important tick species, particularly northward and to higher altitudes, amplifying their global impact on public health (Sutherst 2001; Süss et al. 2008). Several external factors may interact to produce such patterns (Fig. 1a), with a predominant role for climate change due to direct modifications in temperature, rainfall and humidity, and their associated indirect effects on vegetation, host diversity and abundance (Fig. 1b) (Childs et al. 1998; Githeko et al. 2000; Sutherst 2001; Randolph 2004; Gray et al. 2009). As parameters such as temperature and rainfall vary, we are witnessing corresponding changes in tick phenology, survival and development (Eisen et al. 2002; Ogden et al. 2005, 2008; Gray 2008, 2009). For example, the seasonal activity of *Ixodes ricinus*, the European sheep tick (see case study on *I. ricinus* below), usually lasts from March to October, but ticks can now be observed questing during the winter (early November to early March). Moreover, due to increasing mean temperatures, associated increases in metabolic rates, questing periods and host availability, tick development time appears to be shorter, their mortality lower and host exploitation rates higher (Randolph 1997; Ogden et al. 2004; Lindgren and Jaenson 2006; Gray 2008, 2009, also see case studies). Global changes are also responsible for distributional changes towards higher altitudes (Daniel et al. 2003; Danielová et al. 2006, 2008; Gern et al. 2008; Gilbert 2010) and latitudes (Brownstein et al. 2005; Ogden et al. 2006; Lynch et al. 2010; Leighton et al. 2012). For example, the northward expansion of *I. ricinus* has been well-documented in Scandinavia (Fig. 2) (Tälleklint and Jaenson 1998; Lindgren et al. 2000; Jore et al. 2011). *Ixodes uriae*, a tick associated with colonial seabirds, may be increasing in abundance and occurrence at high latitudes (Coulson et al. 2009; Lynch et al. 2010). Expansions have also been observed in African ticks of the genus *Amblyomma* (Estrada-Peña et al. 2008) and *Rhipicephalus* (Olwoch et al. 2007; Madder et al. 2007). Depending on different climate change scenarios, an increase in global habitat suitability over the next 100 years of 1–9 million km<sup>2</sup> has been predicted for nearly all African tick species. Moreover, the potential



**Fig. 1** **a** Relationships among changes in climate, landscape and human activities on the ecology of ticks and tick-borne disease (modified from Lindgren 1998). **b** Schematic illustration of direct and indirect impacts of climate on tick distributions and population densities (modified from Lindgren et al. 2000)

for successful translocations of ticks and their pathogens from Africa to other countries is likely to increase over the same timeframe (Cumming and Van Vuuren 2006).

Numerous studies report expansions in the distributional area of ticks and their associated pathogens, but ticks should also disappear from some places as conditions of temperature and humidity become unsuitable (Cumming and Van Vuuren 2006; Estrada-Peña and Venzal 2006; Lindgren and Jaenson 2006). Few reports exist on the local extinction of ticks. Jones and Kitron (2000) observed that after years of drought in Illinois,



**Fig. 2** Differences in *Ixodes ricinus* tick prevalence and distribution in central and northern Sweden between the 1980s and the 1990s. White dots illustrate districts in Sweden where ticks were reported to be present, **a** before 1980 and **b** after the mid 1990s. The black line defines the study area. The study was made by Jaenson et al. (1994), based on a questionnaire published in several Swedish newspapers, in which they asked questions about ticks from throughout Sweden (data source: Lindgren et al. 2000, Reproduced with permission from Environmental Health Perspectives)

USA, the abundance of *Ixodes scapularis* ticks decreased strongly. A general increase in European regions with a Mediterranean climate has been predicted and should lead to the disappearance of *I. ricinus* in these areas due to a lack of moisture (Estrada-Peña and Venzal 2006). However, for now, it is unclear whether colonization and extinction probabilities in relation to climatic conditions are equivalent for ticks. For example, ticks may be able to adapt to gradual changes in environmental conditions once locally present, but the initial conditions required for successful colonization may be extremely strict. Systematic surveys on the presence and abundance of ticks at regional scales should provide us with more information on such questions (Rogers and Randolph 2006; Hancock et al. 2011).

Other factors, in addition to overall temperature and humidity, may also be important in determining range changes. For example, the reforestation of some landscapes and fragmentation of others can result in variation in micro-climatic conditions and available resources (Foley et al. 2005; Gray et al. 2009) which can lead to changes in the diversity and abundance of ticks and their principal hosts (Jones et al. 1998; Randolph and Storey 1999; Logiudice et al. 2003; Ostfeld et al. 2006; Cumming 2007). Changes in vertebrate host populations may have significant impacts on the ecology and evolution of ticks at different biological scales (individual, population and community). For example, an increase in the population size of a reservoir host species (i.e. that maintains pathogens for transmission to vectors), or of an amplifying host species (i.e. which favours tick feeding success) can result in a significant increase in tick density and in the prevalence of the

diseases they transmit (Gilot et al. 1994; Van Buskirk and Ostfeld 1995; Allan et al. 2003; Logiudice et al. 2003, 2008; Ostfeld et al. 2006; Rizzoli et al. 2009; Gilbert 2010). This has been the case for *I. scapularis* in the USA, where increased habitat fragmentation has been linked to reduced vertebrate biodiversity within habitat patches. Certain vertebrate species, and in particular the white-footed mouse *Peromyscus leucopus* and the eastern chipmunk *Tamias striatus*, are resistant to fragmentation and are therefore more frequently used by ticks within small habitat patches compared to larger patches where other more preferred host species may be present (Schulze et al. 2005; Ostfeld et al. 2006). As these two rodents are excellent reservoirs for Lyme disease spirochetes, this reduction in host biodiversity is thought to lead to a direct increase in Lyme disease occurrence in small patches (Van Buskirk and Ostfeld 1995; Ostfeld and Keesing 2000; Schmidt and Ostfeld 2001; Allan et al. 2003; Logiudice et al. 2003, 2008; Keesing et al. 2006). Likewise, with increases in human movements, and that of domestic livestock and companion animals at a world-wide scale (Weiss 2008; Beugnet and Marié 2009; Barré and Uilenberg 2010), we have seen a direct increase in the number of introductions of ticks and new vertebrate host species to novel areas (Barré and Uilenberg 2010; Pisanu et al. 2010). The invasion of *Rhipicephalus (Boophilus) microplus* to New Caledonia and South Africa, and *Amblyomma variegatum* to the Caribbean via livestock transportation are perfect examples and are discussed below in some detail (see case studies below).

### Consequences of changes in tick distributions

#### Host population dynamics and community structure

With the arrival of a new tick species into a community certain host species may be favoured, whereas others will be disfavoured. Negative consequences on hosts can be due to the direct debilitating effects of ticks on these vertebrates, effects which may include blood loss (Wanless et al. 1997), weight loss (Jonsson 2006), behavioural modifications (Mangin et al. 2003), or secondary skin infections. These changes can lead to reduced survival or breeding performance which may, in turn, alter the dynamics of these populations (e.g. Boulinier and Danchin 1996). Other negative consequences can be indirect, such as transmission of viral, bacterial and/or protozoan pathogens that reduce host survival (Sonenshine 1993). However, more generally, it is difficult to predict the impact of ticks on novel hosts. In some cases, the effect can be large at both individual and population levels. Indeed, novel hosts often show higher tick burdens than original hosts (Pisanu et al. 2010), simply because they have not co-evolved with these ectoparasites and therefore have not developed appropriate responses to cope with infestation. In other cases, ticks may be unable to exploit newly available hosts. However, this type of ‘null’ observation is difficult to make without an experimental approach. More generally, the impacts of invasive ticks on novel host populations and the number of tick generations required for adaptation to a new host have been poorly studied and described (but see case study on *R. microplus* below). This type of information will be essential for predicting the success of new invasions.

The invasion of new tick species may also alter other interactions within the community. For example, in some cases, the arrival of a new tick species may actually have a positive effect on certain vertebrate populations due to apparent competition. Indeed, although poorly studied in ticks, exploitation of one host population by ticks may increase the success of a competing population by placing the exploited population at a competitive



disadvantage (Tompkins et al. 2011). The arrival of an invasive tick can also modify the local success of endemic ticks which have evolved within the community. One of the few (if not only) studies that examines this question was performed by Zeman and Lynen (2010). These authors developed a model of the interaction between the invasive cattle tick *Rhipicephalus microplus* and the native cattle tick *Rhipicephalus decoloratus*. *Rhipicephalus microplus* was introduced to South Africa near the end of the nineteenth century and quickly started to out-compete the native cattle tick *R. decoloratus* (Theiler 1962; Tønnesen et al. 2004). The two tick species differ slightly in their temperature and relative humidity preferences, and by their relative reproductive performance on cattle (i.e. *R. microplus* has higher reproductive success than *R. decoloratus*). They also differ in their preferred hosts; in South Africa, the invasive tick only exploits cattle, whereas the resident tick exploits both cattle and large wild mammals. The model developed by Zeman and Lynen (2010) shows that for simulations to fit observed data, two key factors are required: (1) mutual exclusion between *R. microplus* and *R. decoloratus* that results from increased mortality by shared pathogen(s) and (2) use of wild fauna by *R. decoloratus*, so that this native tick avoids competition with the invasive tick (see case study on *R. microplus* below).

As illustrated by the examples above, the impact of a new parasite on local community structure can be complex. The direct effect of ticks on the hosts and changes in the circulation of pathogens with varying levels of virulence can have long-reaching impacts on local interactions. Models that examine these complex effects may help us better appreciate the consequences of such interactions and the long-term impacts of tick invasions for population dynamics and community structure.

#### Adaptation to novel hosts and the evolution of tick biodiversity

Shifts in tick distributions can result in selection for novel host exploitation. For example, investigations have been made on the cattle tick *R. microplus*, which invaded New Caledonia in 1942, and which quickly adapted to exploit a novel host there, the rusa deer (*Cervus timorensis rusa*). Although initially considered as a poor host for the tick, with low infestation levels and feeding success (Barré et al. 2001), the bovid tick adapted to successfully exploit this host within less than 250 generations and we now see the presence of an independent ‘deer-adapted’ population of this tick on sympatric ranges with the traditional ‘cattle-adapted’ population (de Meeûs et al. 2010; see case study below for more details, see also Chevillon et al., this issue). The same observations have been made in the seabird tick *I. uriae*. This tick was supposed to be a seabird generalist, but observations in several areas of its range have shown that the evolution of host-associated genetic structure may occur repeatedly and rapidly in this system (Kempf et al. 2009a; McCoy et al. 2001, 2005). This type of divergence may lead to distinct locally-adapted populations and may be a key process in the emergence and maintenance of tick biodiversity (Magalhães et al. 2007).

#### Alternations in disease transmission and emergence

Scientists have written extensively about the possible impacts of global changes on emerging and re-emerging infectious diseases (e.g. Shope 1991; Fayer 2000; Sutherst 2001; Patz et al. 2008; Shuman 2010). Increases in tick densities and spatial range can lead to higher prevalence of tick-borne disease. Lyme disease (LD) or Lyme borreliosis is the most prevalent vector-borne disease in the USA and Europe. In both areas, the number of



reported and/or recognized LD cases has increased dramatically since the early 1990s, as has their geographic extent (Childs et al. 1998; Subak 2003; Steere et al. 2004; Hanincová et al. 2006; Lindgren and Jaenson 2006; Gray et al. 2009; Hamer et al. 2010). Similarly, the incidence and distribution of tick-borne encephalitis (TBE), an endemic viral disease in Europe and Asia, has increased significantly over the last 30 years (Lindgren and Gustafson 2001; Daniel et al. 2003; Randolph 2004; Lukan et al. 2010). The increase in both diseases has been attributed to factors that affect vector and reservoir host abundance. For LD and TBE, landscape changes (forest fragmentation in some areas of the USA and reforestation in others, particularly in Europe), are thought to have altered local host community structure, increasing the use of reservoir host species (see Distributional changes in ticks and their causes). On the one hand, such changes may reduce what is termed the ‘dilution effect’ of biodiversity: higher vertebrate biodiversity results in lower pathogen prevalence in questing ticks because ticks feed more on non-reservoir hosts (Van Buskirk and Ostfeld 1995; Ostfeld and Keesing 2000; Schmidt and Ostfeld 2001; Allan et al. 2003; Logiudice et al. 2003, 2008; Keesing et al. 2006). On the other hand, key host populations may increase leading to amplified disease risk. For example, reforestation has resulted in an explosion of populations of deer and wild boar in Europe, species which present high seroprevalence for TBE and provide excellent feeding opportunities for questing ticks (Šumilo et al. 2008). This, in turn, has led to both an increase in tick abundance and disease prevalence (Gilot et al. 1994; Carpi et al. 2008; Rizzoli et al. 2009).

Human life-style changes (settlements, travel, recreational and leisure behaviour, etc.) and the increased worldwide transportation of livestock has resulted in many disease introductions. Recently, diseases such as babesiosis and anaplasmosis, have been reported from countries where they were previously absent. Indeed, increases in the transportation of animals and humans to ever more distant locations provide ideal conditions for the circulation of pathogens, especially when cattle, pets or sport animals are travelling with their owners (Beugnet and Marié 2009). Allan et al. (2010) have shown that even the introduction of invasive plants can have a significant impact on vector-borne disease risk. The Amur honeysuckle (*Lonicera maackii*), a widespread invasive shrub in North America, attracts white-tailed deer, a reservoir of ehrlichiosis and host of the tick vector *Amblyomma americanum*. The attraction of deer to this invasive plant is reflected by a significant increase in the number of ticks infected with the bacterium in patches where the Amur honeysuckle is present. Thus, the introduction of novel plants can lead to an indirect increase in disease incidence.

## Methods to detect distributional shifts and their consequences

Several methods are used by scientists to detect, understand and predict the changing distribution of vectors, reservoirs and pathogens caused by anthropogenic and environmental changes. All have strengths and weaknesses and the choice of study will depend on the nature of the species under question, its distribution and the means available in terms of time, money and expertise.

### Field-based studies

Such studies are, of course, the basis of our knowledge of the natural world and are essential for understanding the general ecology of a species and the factors that affect its presence and abundance in the local environment. Without this baseline information, often

accumulated over time via numerous scientists, other inferential approaches can be largely without value. However, systematic field studies focused on a single species can be difficult to conduct in many cases, particularly over long time periods and by a single research team. Many experts have fragmentary information on the presence of tick species locally, but this information is not always available. Currently, efforts are being made at regional and continental scales to synthesize available data and establish a more public surveillance system. Such is the case of the emerging Vbornet project funded by the European Centre for Disease Control and Prevention (ECDC), which aims to create an active European network of experts involved in entomology and vector-borne public health issues and to use this network to collate historical and current data on vector distributions ([http://ecdc.europa.eu/en/activities/diseaseprogrammes/emerging\\_and\\_vector\\_borne\\_diseases/Pages/VBORNET.aspx](http://ecdc.europa.eu/en/activities/diseaseprogrammes/emerging_and_vector_borne_diseases/Pages/VBORNET.aspx)).

### Molecular genetics

Even with considerable collaborative efforts, field-based studies often remain largely observational and can therefore be limited by the breadth of biological parameters that can be estimated. Indirect techniques, such as molecular methods, can be used to obtain some additional and relatively inaccessible information. Molecular-based approaches, using neutral genetic markers, can provide us with data that can be used to infer how tick populations have changed over time and how they are currently functioning (de Meeûs et al. 2007; Chevillon et al. 2012b). These studies can focus at two time scales: ecological time scales, using markers with fast mutation rates whose structure represents contemporary demographic events (e.g. microsatellites), or more evolutionary time scales, using markers that inform us about more historical population events (e.g. often sequence-based data). This latter time scale is typically the focus of phylogeographic studies that aim to combine genetic and biogeographic data in order to identify the processes responsible for contemporary patterns of species distributions (Avise 2000). As population-level structure largely depends on the balance between genetic drift (i.e. the random sampling of genetic variants) and gene flow, genetic data can provide otherwise cryptic information on the distinctness of populations, the distance and direction of historical gene flow, the origin of ticks in newly colonised areas and the nature of this colonisation event (see case study on *R. microplus* below for an example).

Landscape genetics is a relatively new framework for studying the population structure of a species and identifying the link between this structure and the various environmental factors that may condition it (Storfer et al. 2007). This approach incorporates tests of landscape heterogeneity on gene flow and genetic variation within and among populations. Landscape genetics can help identify barriers to dispersal, infer the effect of landscape change on genetic diversity, identify migrants in relation to landscape, estimate source-sink dynamics, and compare observed genetic patterns between contemporary and historic landscapes (Storfer et al. 2010). These data can then be used to predict the spread of disease or invasive species.

Molecular-based approaches can also focus on parts of the genome under selection. This can be particularly important if recently established populations differ in ecological characteristics that are important for host exploitation and disease transmission. For example, the evolution of acaricide resistance is a recurrent problem for controlling cattle ticks (Chevillon et al. 2007; Cutullé et al. 2009). Combined with experimental approaches, molecular genetics could, for example, inform us on the nature of this resistance, the number of times it may have evolved within a given region and, when combined with data

from neutral genetic markers, its potential to spread to new populations. This information thus provides important elements for understanding the potential invasiveness of a given species.

Today, powerful new genetic approaches can also provide us with critical information on host use by ticks. Due to the difficulty in trapping vertebrate species, ticks are often sampled in the questing phase, with no information on previous host use or potential host preferences. To understand tick population dynamics and structure, and their link to pathogen transmission, it is essential to establish the contribution of different local host types to tick feeding. New molecular techniques are now available to detect host blood-meal remnants in hematophagous arthropods (Kent 2009). Thus, it is possible to identify the last host of unengorged questing ticks, without directly collecting on the host. Several new techniques are being used for different arthropod species (see Kent 2009 for a review), but work in ticks has to date been based solely on reverse line-blot (RLB) hybridization (Pichon et al. 2003; Morán-Cadenas et al. 2007; Allan et al. 2010). RLB techniques have the advantage of being able to identify the host to the species level, but remain relatively difficult to set-up and run in routine. Other techniques, such as Real-Time multiplexed PCRs, which use specific probes for up to four targeted taxa, may be a viable alternative for tick systems, as they can simultaneously identify the host and detect mixed bloodmeals. Such approaches can also be used to determine the frequency, quantity and nature of infection with different microparasites and pathogens in ticks. For example, a highly sensitive target-specific qPCR procedure can be used first to detect pathogens in ticks, and then to quantify relative differences in infection among different host-associated tick groups (Gómez-Díaz et al. 2010).

### Predictive modelling

Once the basic ecology of a species has been established, modelling can be used to make predictions about how tick populations and their interaction networks may change over time and space. The establishment of a viable tick population will only occur if environmental conditions are favourable. Researchers are now using complex mathematical or statistical modelling to predict these potential areas of installation, to define its contours and its evolution under different scenarios of climate change (e.g. Sutherst 1998, 2003; Sutherst et al. 2007; Ogden et al. 2005; Rogers and Randolph 2006; Olwoch et al. 2007; Vourc'h and Vial 2008; Sutherst and Bourne 2009). These studies have mostly been initiated by Sutherst and Maywald (1985) with their CLIMEX model.

There are currently two types of models to predict tick distributions: pattern-matching (or statistical or associative) models and process-based (or mechanistic or biological) models (Vourc'h and Vial 2008). Both have their foundation in ecological niche theory, which considers the niche as an n-dimensional hypervolume where the dimensions are environmental conditions that define the range in which a species can persist (Hutchinson 1957). In the pattern-matching model, the currently observed distribution is matched to climate variables in a statistical framework. Then, the projected change in climate variables is applied to the distribution by interpolation or extrapolation. The process-based model is more biologically-based and seeks to describe the processes involved in the changing distribution of ticks and how they can be affected by climate (Vourc'h and Vial 2008). For example, both approaches have been used for *Hyalomma marginatum marginatum*, one of the most important tick vectors of Crimean Congo Hemorrhagic Fever virus (CCHF) in the Mediterranean Basin. In Turkey, CCHF disease emerged in 2002. Estrada-Peña et al. (2007b) used data on reported tick presence and the occurrence of

CCHF cases in this country for statistical modelling and showed that the risk of CCHF occurrence could be predicted by climatic conditions (temperature, rainfall and evapo-transpiration) that constrain tick presence, and by landscape fragmentation that reflects interface zones for transmission. This statistical tick model has now been extended to the whole Mediterranean Basin and compared to a mathematical population model in order to better describe the processes underlying the effect of climate on tick survival, development and seasonal dynamics (Estrada-Peña et al. 2011). In parallel to both statistical and mathematical approaches commonly used by modellers, the fuzzy set theory (Zadeh 1965) and multi-criterial decision analysis (MCDA) methods have emerged as alternative ways of ecological modelling (Bock and Salski 1998, Adriaenssens et al. 2006). Such methods are verbal models based on the integration of expert knowledge and bibliographic data to determine a small set of major rules that best characterize a tick species under known environmental constraints. This method may be promising for a rapid assessment when presence/absence data and our knowledge on the biological characteristics of the tick species in question are limited (Vial 2009).

The utilization of predictive models has been favoured by development of geographic information system (GIS) software and satellite-based sensors which have improved data mapping and climate data collection. Several climatic scenarios have now been published by the IPCC (Intergovernmental Panel on Climate Change) for the future. However, to better understand the changing distributions of tick populations and to detect their expansion, their distribution prior to climate change is theoretically needed. This is rarely available (see above). There also remains the problem of missing data due to systematic sampling in some places—mainly where tick-borne diseases are most prevalent—and the absence of sampling in other places. Finally, attention must be paid to the fact that tick distributions may be affected by factors other than climate. Indeed, for endophilous tick species, their microhabitat may buffer wider scale climatic changes in a way that may be difficult to predict (Vial 2009). As mentioned previously, for many tick species, their presence, abundance and dynamics may largely rely on that of their hosts. Therefore, to understand and predict how tick populations are connected and how their associated pathogens are exchanged, one requires specific data on host movement in the landscape (e.g. McCoy et al. 2003; Vollmer et al. 2010). The new challenge for modelling is therefore how to spatially quantify landscape networks in relation to host movements and how to predict their change. Indeed, more detailed data on local interactions may allow us to model tick-borne disease transmission scenarios, which take into account dynamic biological processes rather than simply the likelihood of occurrence of a tick species based on climate suitability (Kalluri et al. 2007; Sutherst et al. 2007; Estrada-Peña 2008).

## Case studies

We have chosen three examples to illustrate how the changing distributions of ticks and their invasion into new areas of the world can have major impacts for humans and their livestock. These examples are far from exhaustive, but are among the best documented.

### Invasion of the tropical and sub-tropical belts by the southern cattle tick

The southern cattle tick *R. (B.) microplus*, initially a parasite of Asian bovid species (Osterkamp et al. 1999; Barré and Uilenberg 2010) in India and Indonesia (Labruna et al. 2009), has spread over the tropical and subtropical belts to become a major pest in many

agrosystems (Frisch 1999; see Barré and Uilenberg 2010 for a recent review) (Fig. 3). Its current geographic distribution and its dramatic expansion over the last 150 years can primarily be explained by the introduction of European cattle (*Bos taurus*) to tropical areas. In contrast to tropical Bovidae, these introduced hosts of European origin are almost incapable of mounting efficient immune responses to *R. microplus* infestations (Frisch 1999). Other factors may have constrained the geographical distribution of *R. microplus*, such as competition with other tick species (Tønnesen et al. 2004; Zeman and Lynen 2010) and/or climate variables, as has been described for other ticks (Estrada-Peña et al. 2005; Cumming and Van Vuuren 2006; Olwoch et al. 2007), but these constraints seem to have only a limited effect on the colonisation potential of this tick species.

Understanding the demographic functioning of *R. microplus* populations may help explain the invasiveness of this species. Indeed, *R. microplus* is a one-host (monotropic) tick, meaning that all life stages remain on the same individual host (two moults and mating). Only the female drops to the ground after her bloodmeal to lay eggs. After hatching, the larvae then find a new host individual. This type of life cycle can result in a rapid increase in tick population size after colonising an appropriate host. On the island of New Caledonia, the invasion history of this tick has been well-characterized. In 1942, a few *R. microplus* individuals were accidentally introduced to the island with livestock imported from Australia (Rageau and Vergent 1959). The absence of the southern cattle tick prior to 1942 and the drastic quarantine measures taken after are well-documented (Bennett 2004) and have been confirmed by two complementary genetic analyses (Koffi et al. 2006; Labruna et al. 2009; more detail on the use of population genetics to characterise the demographic functioning of *R. microplus* can be found in the review by Chevillon et al., this issue). The high susceptibility of *B. taurus* breeds raised in New Caledonia, coupled with the mild climatic conditions that allow year-round activity, have favoured a rapid invasion of all local cattle herds. Although these ticks have been largely



**Fig. 3** Current geographical distribution of *Rhipicephalus* (*Boophilus*) *microplus* (in black), with recent observations of the tick in Western Africa (black circle) (Madder et al. 2007). This 1-host tick has a high invasion potential into areas where European cattle breeds have been introduced. Once established, it can vector important livestock parasites, and notably different species of *Babesia* (modified from Barré and Uilenberg 2010)

pathogen-free, blood loss and irritation from bites can result in significant weight loss and reduced livestock production. The local authorities therefore decided to freely deliver acaricide chemicals to farmers, starting with arsenic (1943–1950) and DDT (1947–1973). Synthetic pyrethroids (SP), organophosphate compounds (OP), and amitraz were then sequentially distributed. Interestingly, this chronological sequence of acaricide use was followed by the sequential appearance of resistance to each chemical (Brun et al. 1983; Beugnet and Chardonnet 1995; Ducornez et al. 2005). Given that the local tick populations recently descended from a few introduced ticks (Koffi et al. 2006), mutations conferring resistance do not seem to be a limiting factor for *R. microplus* when infesting highly susceptible hosts (Chevillon et al. 2007). The adaptability of this tick is also demonstrated by its capacity to readily exploit new hosts. For example, the *R. microplus* populations of New Caledonia have also been able to adapt to a novel host species, the rusa deer (*Rusa timorensis*). Deer-adapted tick populations, genetically divergent from the cattle tick populations, are now found on the island in areas sympatric with infested cattle (de Meeûs et al. 2010).

The consequences of the dramatic expansion in the geographical distribution of *R. microplus* across tropical and subtropical regions are three-fold. First, in addition to the direct effects it imposes on infested livestock, it also indirectly causes economical losses by vectoring severe diseases such as babesiosis and anaplasmosis (Estrada-Peña 2001; Barré and Uilenberg 2010; Sanders et al. 2010). Second, its propensity to express acaricide resistance has increased control costs due to increases in the chemical doses sprayed on cattle and higher investments in developing effective formulations. These two aspects alone make *R. microplus* a great threat to the worldwide livestock industry. Indeed, *R. microplus* and *R. annulatus*, vectors of babesiosis or cattle fever in the USA, were eradicated at an estimated cost of \$3 billion in equivalent 2007 US dollars (CFSPH 2007). Finally, the invasion of *R. microplus* may also disrupt vertebrate-tick-micropathogen communities in the introduced areas. These interactions have been intensively studied in South Africa with attention given to the relative role of climatic factors, life history traits, vector competence, as well as to direct and indirect interactions between the invasive tick (*R. microplus*) and native cattle ticks (*R. decoloratus*). *Rhipicephalus microplus* was introduced to South Africa at the turn of the 20th century. In the early 1900s, it had already started to invade and out-compete the native cattle tick *R. decoloratus* in cattle herds of the Cape Province (Theiler 1962). Later, outbreaks of Asiatic heartwater (caused by *Babesia bovis*) were used as indicators of the progression of the *R. microplus* invasion. *Rhipicephalus decoloratus* is not a competent vector of *B. bovis*, although both the native and invasive ticks are vector competent for the native *Babesia bigemina* species. Zeman and Lynen (2010) recently developed an integrative model to study the requirements for a stable coexistence of the two tick species. Land use, and especially the conservation of wildlife habitats, appear much more important than climatic change in regulating the interactions between invasive and native ticks and, hence, in determining the epidemiology of invasive and native *Babesia* pathogens.

Two main lessons emerge from the knowledge acquired on the history, cause and consequences of *R. microplus* distributional changes. First, climate change may have very little impact compared to more direct human choices on international livestock exchanges and/or land use. Second, once introduced to areas with susceptible cattle, this tick can rapidly reach large population sizes and can easily adapt to a wide array of new environmental conditions. This highlights the absolute importance of establishing severe quarantine measures, and of developing alternatives to intensive pesticide control programs such as (1) the use of quantitative genetics to improve cattle resistance to *R. microplus*



infestation (Frisch 1999; Constantinoiu et al. 2010; Jonsson et al. 2010), or (2) the use of more traditional agricultural techniques to reduce *R. microplus* larval survival in pasturelands (Hernández et al. 2000; Corson et al. 2001, 2003).

### Distribution shifts in the *Ixodes ricinus* species complex

The *I. ricinus* species complex is composed of 14 species distributed worldwide, the best known of which are *I. scapularis*, *I. ricinus*, *I. persulcatus* and *I. pacificus* (Fig. 4). Many, if not all, of the ticks of this complex are important vectors of human and livestock diseases, including Lyme borreliosis, tick-borne encephalitis, anaplasmosis and babesiosis. Given the strong dependence of these ticks on both the biotic and abiotic components of their environment, their distribution has undergone major changes over the last decade in correspondence with changing landscapes and climate. Here, we present the specific cases of *I. scapularis* and *I. ricinus*. Due to their major role in the transmission of Lyme borreliosis in, respectively, the USA and Europe, these species are by far the most studied of the complex.

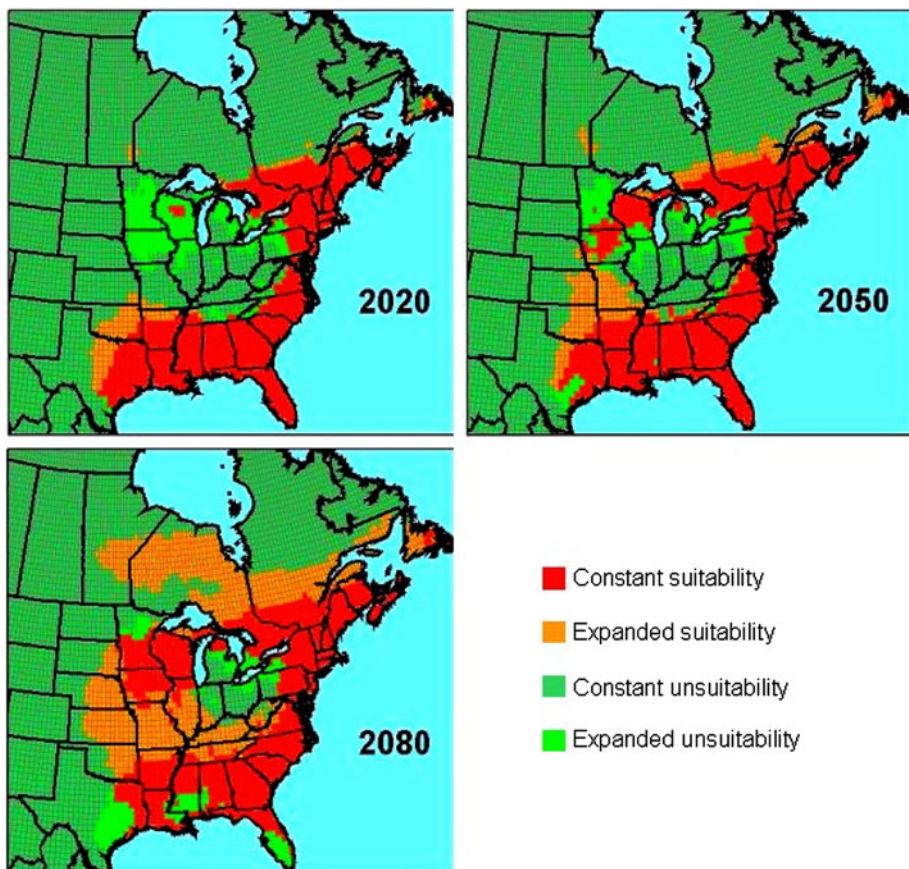
The black-legged tick *I. scapularis* is responsible for the transmission of a range of diseases in eastern North America: human granulocytic anaplasmosis, human babesiosis and Lyme disease. Lyme disease alone, caused by infection with spirochetes of the complex *Borrelia burgdorferi* sensu lato, represents more than 90 % of all reported cases of vector-borne diseases in the USA and constitutes a major public health threat (Thompson et al. 2001; Bacon et al. 2008). Within the past years, a rapid spread of *I. scapularis* into many parts of the Midwest and northeastern USA and southeastern Canada has been observed (Wilson 1998; Steere et al. 2004; Hamer et al. 2010; Leighton et al. 2012). Large increases in white-tailed deer (*Odocoileus virginianus*) populations, the primary hosts for adult ticks, are considered to have facilitated the expansion of the tick and the emergence of Lyme disease. The explosion of these deer populations over the last



**Fig. 4** The approximate geographic distribution of the four most studied ticks of the *Ixodes ricinus* species complex. The area in black represents an over lap in the distribution of *I. ricinus* and *I. persulcatus* (modified from Swanson et al. 2006)



50 years has been related to changes in land use patterns, notably a reversion of agricultural lands to new-growth forests with extensive edge, and to restrictions on hunting (Gubler et al. 2001; Steere et al. 2004). The invasion of *I. scapularis* has also been proposed to be linked to higher temperatures and shorter winter freeze periods which has opened up new suitable environments for these ticks and allowed them to increase in abundance (Githeko et al. 2000; Gubler et al. 2001; Estrada-Peña 2002; Brownstein et al. 2005; Ogden et al. 2008). Several models, based on projections of climate change, predict that *I. scapularis* abundance will increase over time and its expansion will continue northward (Fig. 5) (Brownstein et al. 2005; Ogden et al. 2005, 2006; Diuk-Wasser et al. 2010; Leighton et al. 2012). Such projections are worrisome, particularly given that recent studies have shown that dispersal barriers to pathogens, such as Lyme spirochetes, tend to be much lower than those of their tick vectors (Humphrey et al. 2010; Gómez-Díaz et al. 2011). This means that once established in a new location, associated pathogens may emergence in a short period of time.



**Fig. 5** Projected distribution of climate-based habitat suitability for *Ixodes scapularis* for three future periods (2020s, 2050s, 2080s). The simulation is based on climate change predictions using the Canadian Global Coupled Model (CGCM1) produced by the Canadian Centre for Climate Modelling and Analysis. Anticipated increases in both greenhouse gas and sulfate aerosols were integrated in the model (modified from Brownstein et al. 2005)

*Ixodes ricinus* (also called the Sheep tick or the Castor bean tick) is wide-ranging in Europe (Fig. 4) and transmits an even greater array of pathogens than its sister species in North America (Lindgren and Jaenson 2006; Gray et al. 2009). As *I. scapularis* and some other temperate tick species, *I. ricinus* has a high affinity for humans, making it the most important bridging vector in Europe (Guiguen and Degeilh 2001; Parola and Raoult 2001). Climate is regarded as the principal factor limiting *I. ricinus*'s distribution, in addition to its seasonal activity, its development and associated disease incidence (Daniel 1993; Jaenson et al. 1994; Lindgren et al. 2000; Estrada-Peña and Venzal 2006; Gray 2008; Gilbert 2010). Since the 1980s, we have witnessed the colonization of new areas by *I. ricinus*, and a general increase in its abundance. Tälleklint and Jaenson (1998) and Lindgren et al. (2000) suggest that milder winters have led to a range expansion of *I. ricinus* northward into Sweden (Fig. 2). Similar conclusions have been made to explain a shift of ticks toward higher altitudes (Daniel et al. 2003; Danielová et al. 2006, 2008; Gern et al. 2008; Gilbert 2010). Changes in vegetation, reforestation and the replacement of trees such as spruce with beech or oak, are also thought to improve both tick microhabitat conditions and the abundance of favourable host species, such as deer and rodents, contributing to an augmentation in the over-density of *I. ricinus* (Gilot et al. 1994; Boyard et al. 2007; Carpi et al. 2008; Rizzoli et al. 2009). Along with increased densities, we have also seen a correlated increase in cases of Lyme disease and tick-borne encephalitis (see section 'Alternations in disease transmission and emergence'). About 85,000 cases of Lyme disease are now reported annually in Europe (Lindgren and Jaenson 2006) and the reported incidence of tick-borne encephalitis increased by 400 % between 1974 and 2003 (Süss 2008). However, it remains unclear whether increases in disease incidence are due to an increased number of ticks, their range expansion, or increased awareness in the general population and among medical personnel.

Another factor that is thought to favour the expansion of *I. ricinus*, and other species of this complex, is its generalist nature in terms of host exploitation. However, recent work on the population genetics of *I. ricinus* suggests that some specificity may evolve in these populations. In particular, patterns of mate choice suggest the presence of assortative mating in some populations (Kempf et al. 2009b). Similarly, the possible existence of a Wahlund effect (i.e. a sub-structuring within a population) due to differential host use within populations has been suggested to explain repeated observations of heterozygote deficits within populations (de Meeûs et al. 2002; Kempf et al. 2010, 2011). Since pathogen transmission depends on both the distribution and host use of the vector, predicting how the expansion of *I. ricinus* will impact disease transmission will depend on our knowledge of the plasticity of host use by this tick and its relatives.

### Successive invasions by *Amblyomma variegatum*

The tropical bont tick *A. variegatum* is a three-host tick which infests livestock and wildlife. It is among the most harmful tick species because it impairs animal growth and can cause severe wounds to cattle (Stachurski 2000). Moreover, it is host to a number of microbial pathogens. As other ticks of the genus *Amblyomma*, *A. variegatum* can vector heartwater (or cowdriosis), a fatal rickettsiosis of European cattle caused by *Ehrlichia ruminantium* (Uilenberg and Camus 1993), and *Rickettsia africae*, the agent of African tick-bite fever. Its saliva also favours the development of severe acute dermatophilosis, a bacterial skin disease of animals caused by *Dermatophilus congolensis* (Barré and Uilenberg 2010).

*Amblyomma variegatum* is the *Amblyomma* species with the largest distribution in Africa, present in more than 30 countries (Fig. 6a) (Cumming 1999). Several life history traits may be linked to the overall success of this tick: it can withstand long periods waiting for a favourable host (over 20 months for an unfed female) and once fed, she can produce an astounding 20,000 eggs (Barré and Garris 1990). Moreover, *A. variegatum* occupies a great diversity of habitats, from grassy steppes and mountain meadows to wet savannas on the edge of the rainforest. This great ubiquity, coupled with its biology and its marked affinity for livestock, has facilitated its spread outside of its native range (Estrada-Peña et al. 2007a). Indeed, from its native Africa, *A. variegatum* has colonized several zones: Caribbean (Fig. 6b), Madagascar, the Comoro and Mascarene Islands (Fig. 6a) and Yemen (Barré and Uilenberg 2010). It is now considered the second most invasive tick species after *R. microplus* (Barré and Uilenberg 2010).

*Amblyomma variegatum* colonized the Caribbean during the nineteenth century; there is no doubt that it was imported with cattle from Senegal, Gambia and Guinea. It first established successfully in Guadeloupe in 1828–1830 and then colonized Marie-Galante, Antigua, and Martinique (1948). Then, between 1967 and 1988, *A. variegatum* colonization reached 14 islands (Saint Croix, Saint Vincent, La Desirade, Saint Lucia, Saint Kitts, Anguilla, Dominica, Barbados, Saint Martin, Montserrat) (Fig. 6b) with the transportation of zebus, goats, dogs, cattle, hides, etc. (Barré et al. 1995; Maillard and Maillard 1998). However, the dissemination of *A. variegatum* across the Caribbean cannot be solely explained by livestock movement around the islands. The spread may also be related to the rapid expansion, starting at the beginning of the 1950s, of cattle egret populations (*Bubulcus ibis*), a very typical host to this tick (Corn et al. 1993; Barré et al. 1995).

Because of its capacity to colonize new areas, including areas that have become suitable due to climate warming (Estrada-Peña et al. 2007a), and considering its medical and



**Fig. 6** The current geographical distribution of *Amblyomma variegatum*. **a** This tick originated in Africa but has now been introduced to Madagascar and The Mascarene (modified from Cumming 1999). This species has also been recently observed in Yemen (black circle) (Barré and Uilenberg 2010). **b** In the eastern Atlantic, *A. variegatum* was introduced to the Lesser Antilles where it has quickly spread despite control attempts (grey circle)

veterinary importance, the eradication of *A. variegatum* from the Caribbean, and the prevention of inter-island movements of livestock, is required to reduce its impact on local agro-ecosystems and prevent its continued invasion (Barré et al. 1995). An eradication programme (Caribbean *Amblyomma* Programme) was started in the Lesser Antilles in 1994 (Pegram et al. 1997), but was abandoned in 2006 because of high costs and difficulties in reaching objectives (Pegram 2006). Currently, re-infestation foci have been reported on Caribbean islands previously classified as provisionally *A. variegatum*-free (Molia et al. 2008). Despite acaricide treatments and quarantine measures, these ticks are continuing to spread among Caribbean Islands and may continue onto the American continent (Estrada-Peña et al. 2007a; Molia et al. 2008). If the invasion of this tick is to be effectively controlled, an improved tick control strategy is required, along with a better understanding of tick dispersal mechanisms, and particularly the role of birds such as the cattle egret in among island movements.

## Conclusions and futures avenues

Due to their only partial dependence on the host environment, ticks are very sensitive to global changes related to landscape, climate and vegetation, changes that are occurring at an ever-increasing rate. In tandem with these effects, the frequent large-scale movements of humans and their animals may be speeding up the introduction of novel tick species and their associated pathogens. Range expansions of these vectors can alter local ecological interactions within communities and may favour the emergence of novel disease (Fig. 1a, b). However, determining the precise factors that influence the distribution of ticks, and their relative importance, can be difficult; for example, in some cases climate change may have less impact than host movements (Fig. 1) (Lindgren and Jaenson 2006; Rogers and Randolph 2006). An important consideration is that even small changes can have major impacts: the exploitation of novel hosts can lead to changes in local species interactions, can alter pathogen virulence, and result in the emergence of novel pathogen strains. Modifications in the population functioning of ticks mean that estimations of disease risk and the efficacy of control measures may be altered and difficult to predict without detailed models.

For now, we have only fragmentary information on the current distribution of ticks and pathogens. Moreover, there is clearly a lack of studies on the impact of tick invasions on local interactions with hosts, the nature of tick adaptations to new environments and, the damage this may have on the established community of hosts and ticks. Recent studies on invasive ticks have suggested a remarkable ability of ticks to adapt to modifications in their environment, regardless of whether these modifications are related to host use, acaricide use or climate change. A concerted effort is therefore required to establish reliable distribution maps that can mark the starting point for following temporal changes in species distributions. Continent-wide projects, such as the ECDC's VBORNET, should go a long way in this direction, and improve our ability to respond to the potential risk of disease emergence. Likewise, because new tools such as genetic markers, bloodmeal analyses, and statistical modelling are now available, and our abilities to rear ticks under controlled laboratory conditions have improved, we should also be able to obtain a better understanding of the biological mechanisms underlying successful tick invasions and their adaptation to local conditions once established. Using the ensemble of this data, we should then be able to construct a general picture of how future modifications in climate and landscape will affect tick populations, their associated pathogens and the costs of these changes for human societies.

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