

Host–parasite distribution patterns under simulated climate: implications for tick-borne diseases

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ABSTRACT: Ticks are known to depend intimately on both climate and the presence of suitable animal host populations for reproduction, survival and population establishment. In response to the reported probable impacts of climate change on ticks and tick-borne diseases, current and future predicted distribution maps of ticks and animal species have been produced. However, there have been no known attempts to link climate change, the predicted future distribution of ticks and the vertebrates that act as hosts and/or reservoirs for ticks and tick-borne diseases. Yet knowledge of this link provides an in-depth understanding of the impacts of climate change on this complex system. Using a modelling approach, this paper provides the predicted change in distribution range of an economically important tick, *Rhipicephalus appendiculatus* and ten vertebrate species that act as its hosts. Results obtained using a predictive species model and climate variables provided by a nested regional climate model, Division of Atmospheric Area Model (DARLAM) show reduction in tick-range and statistically significant differences between the current and future predicted ranges (probability of occurrence) for individual host species. The results also demonstrate a reduction in the range of the total host assemblage while the ranges of hosts intimately involved in East Coast fever (ECF) transmission were altered to different degrees in different areas in sub-Saharan Africa. Increased probability of occurrences for the tick-host assemblage was predicted in Tanzania, Angola and Mozambique. The implications of these results for future tick abundances and ECF transmission under a changing climate scenario are discussed using the Lyme disease ‘dilution effect’ model. Copyright © 2008 Royal Meteorological Society

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1. Introduction

The two principal requirements for a successful tick population are known to be a suitable environment for the survival of the free-living stages and the presence of suitable hosts in sufficient numbers (Norval and Lightfoot, 1982). The specific environmental and climatic requirements of ticks are well documented in field studies (Norval *et al.*, 1992; Okello-Onen *et al.*, 1999 and in modelling exercises Estrada-Pena, 2003; Olwoch *et al.*, 2007). These and other previous studies have undoubtedly emphasized that a suitable climate is key to influencing the distribution of ticks and that temperature and rainfall are the key determining climatic factors. Temperature determines rates of invertebrate development, reproduction and mortality, and any decrease in temperature could accelerate rates of population increase, especially in areas where these are currently limited by high temperatures (Sutherst, 1996) through reduction in death of eggs by desiccation. Depending on a specific area, an increase in temperature may result in favourable

conditions for ticks’ establishment. Under a range of climate change scenarios, significant range alterations for ticks have been postulated (Estrada-Pena, 2003; Olwoch *et al.*, 2007).

However, ticks exhibit a dual lifestyle in which they must constantly alternate between hiding in protected spaces and climbing up vegetation in a quest to obtain suitable hosts (Londt and Whitehead, 1972). In a given environment, it can therefore be assumed that the density of suitable hosts must exceed a certain threshold level before a tick population can become established (Estrada-Pena, 2003). Moreover, it follows that this host density threshold must increase as environmental suitability declines to compensate for increased mortality in the free-living stages of the ticks i.e. lower tick survival rates must be counteracted by increased probability of finding a suitable host. Nevertheless this rarely happens since as environmental suitability declines, habitat fragmentation increases putting the higher vertebrates at risk but favouring the small mammals resulting in more tick numbers.

The question is how do tick-host dynamics under changing climate affect tick abundance and tick-borne diseases transmission? The phenomenon known as the

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'dilution effect' (Ostfeld and Keesing, 2000a; Schmidt and Ostfeld, 2001) assumes that communities of hosts characterized by high species richness or evenness are likely to contain a higher proportion of hosts that are inefficient or weak in transmitting the disease agents to a suitable feeding vector. The greater the abundance of weakly competent reservoir species, the stronger is the 'dilution effect' and the lower is the probability of disease transmission from any particular bite. However, these communities of weakly competent reservoirs could increase the density of vectors by providing the vector population with more feeding opportunities than they would have in species poor communities. Thus more diverse communities of incompetent hosts could simultaneously decrease infection prevalence and increase the population density of vectors, with unpredictable net effects on disease risk in humans and livestock (Schmidt and Ostfeld, 2001). As climate is one of the most important factors that influence the distribution of both hosts and ticks, an understanding of the impacts of climate change on the tick/host/disease interface is vital in order to achieve more sustainable tick-borne disease control that takes into account the ecological and climatic determinants.

In this paper modelling is used to explore how climate change may affect the distribution of the tick, *Rhipicephalus appendiculatus*, its preferred vertebrate hosts and deduce the implications of this change to the tick-borne disease, East Coast fever (ECF). The latter was used as a model system because it is the most economically important tick-borne disease in sub-Saharan Africa (Okello-Onen *et al.*, 1999) and because the natural history of the pathogen (*Theileria parva*), the primary tick vector (*R. appendiculatus*) and its vertebrate hosts are all relatively well understood (Walker *et al.*, 2000). Consequently, this paper presents (1) the predicted change in current and future climatic suitability of African environments for *R. appendiculatus* and its suit of vertebrate hosts (2) assessment of anticipated tick and host assemblage changes, and (3) use of the 'dilution effect' model to derive the likely implications of these responses to climate change for tick abundances and ECF prevalence in sub-Saharan Africa.

2. Materials and methods

2.1. Study area

This study covers sub-Saharan Africa divided into 3000 grids cells of 60 × 60 km resolution determined by the nested climate model Division of Atmospheric Research limited-area model (DARLAM) (Engelbrecht *et al.*, 2002).

2.2. Species distribution data

Distribution data for *R. appendiculatus* were collated from three datasets. The first dataset (Cumming, 1999) was the principle data set. It provided point localities of exact locations where the ticks were collected in sub-Saharan Africa. This original data set was itself compiled

from many sources. The second data set used was Walker *et al.* (2000). This book provides well illustrated distribution maps of the tick species and was mainly used to gain clarity on a few ambiguous localities contained in the Cumming (1999) data set. The last data were kindly provided by Prof. Ivan Horak from the Onderstepoort Veterinary Institute. These data, also in point localities, represent the most recent distribution points for the tick species. Data congruency was sought from the three datasets and where conflicts were encountered the most recent dataset was used.

2.3. Host distribution data

The distribution data of indigenous host species were obtained from a Databank for the Conservation and Management of the African Mammals (AMD) (Boitani *et al.*, 1999). The 'original data' about host distributions were obtained from numerous published maps and converted into Geographic Information Systems (GIS) (Arc/Info, ESRI, USA) polygon coverages. Known extent of occurrence of the species on which all stages of development for the tick species had frequently been collected, the so-called 'preferred host group', was used in this study (Boitani *et al.*, 1999). These species include domestic cattle (*Bos indicus*), African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), sable antelope (*Hippotragus niger*) impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus*). The African buffalo (*S. caffer*) is also a reservoir of *T. parva* infection. Furthermore, the extent of occurrences of those host species that support only the immature tick stages (Walker *et al.*, 2000) were used, namely, *Lepus capensis* (Cape or brown hare), *Lepus saxatilis* (Scrub hare) and *Lepus victoriae* (African Savanna hare). This was to account for the total impact of changes of numbers of hosts *per se*, which can also influence tick abundances (Horak *et al.*, 2000).

2.4. Climate data

The climate data were obtained from simulations of the high resolution regional limited-area model DARLAM (Engelbrecht *et al.*, 2002). DARLAM was developed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Melbourne, Australia, for use in both short-term mesoscale atmospheric studies and longer-term climate simulation experiments (Walsh and McGregor, 1995). The model is a two-time-level, semi-implicit, hydrostatic primitive equations model. It uses an Arakawa staggered C-grid (Mesinger and Arakawa, 1976) and semi-Lagrangian horizontal advection (McGregor, 1993) with bi-cubic spatial interpolation, and has 18 horizontal sigma (σ) levels in the vertical (Phillips, 1957). DARLAM employs a wide range of physical parameterization schemes to represent atmospheric processes such as cumulus convection that exist at sub-grid scale. A one-way nesting technique (Davies, 1976) is used with lateral boundary conditions supplied by the CSIRO-9 Mk 2 GCM with R21 spectral resolution. In the present study nine separate 30-day simulations were performed for both

January (representing mid-summer conditions) and July (representing mid-winter conditions).

The simulations were performed at a horizontal grid resolution of 60 km × 60 km using a domain of 100 × 100 grid points that covers sub-Saharan Africa. The periods selected are the 1990s and the 2020s. The monthly average of the ten simulations constitutes the model climatology for the month. The CSIRO Mark 2 GCM was used to force DARAM at its lateral boundaries. The GCM was integrated for the period with greenhouse gas forcing corresponding to the A2 SRES (Special Report on Emission Scenario, issued by the Intergovernmental Panel on Climate Change) scenario. The DARAM simulations used here were performed by our colleagues in the Department of Geography, Geo-informatics and Meteorology at the University of Pretoria on a Pentium III workstation with two 550 MHz processors as reported in Engelbrecht *et al.* (2002). Six climate variables (mean, maximum, and minimum of rainfall of January and July that are known to influence the distribution of species) were selected. The validity of these climate variables was assessed in predicting ticks (Olwoch *et al.*, 2003, 2007) and in this study when the predicted current distribution of African buffalo was compared with the known extent of occurrence ($\geq 50\%$ probability of occurrence), more than 90% of the predicted range corresponded with the known extent of occurrence (Figure 1).

2.5. Predictive species model

A simple climate envelope model was used to predict the current and future distribution of the focal species. This model has been previously used in predicting the impacts of climate change on South African biodiversity (Erasmus *et al.*, 2002) and ticks (Olwoch *et al.*, 2003, 2007). Reliable presence records of the ticks were selected and the present climate values at these locations were used to construct a climate envelope that represented the range of climates within which a particular tick is known to occur. To arrive at a predicted distribution under a climate change scenario, the existing climate envelope is applied to a climate surface representing future climates, and a new geographical interpretation of distribution is derived.

2.6. Modelling the distribution of ticks and hosts

The input data comprised 3000 grid cells covering sub-Saharan Africa populated with climate variables. Thus, on a scatter plot of climate variables (multivariate climate space), the values of climate variables, from localities where species had been recorded, were used to construct a confidence region where there was a high probability that the records reflected the core range of the species. Points falling within this confidence region were mapped back to geographic space to represent an *interpolated distribution* (ID), represented as a probability of climate suitability ranging from 0 to 1 (0–100%). The resultant probability of occurrence was used to draw maps of climatic suitability. Modelling species distribution in

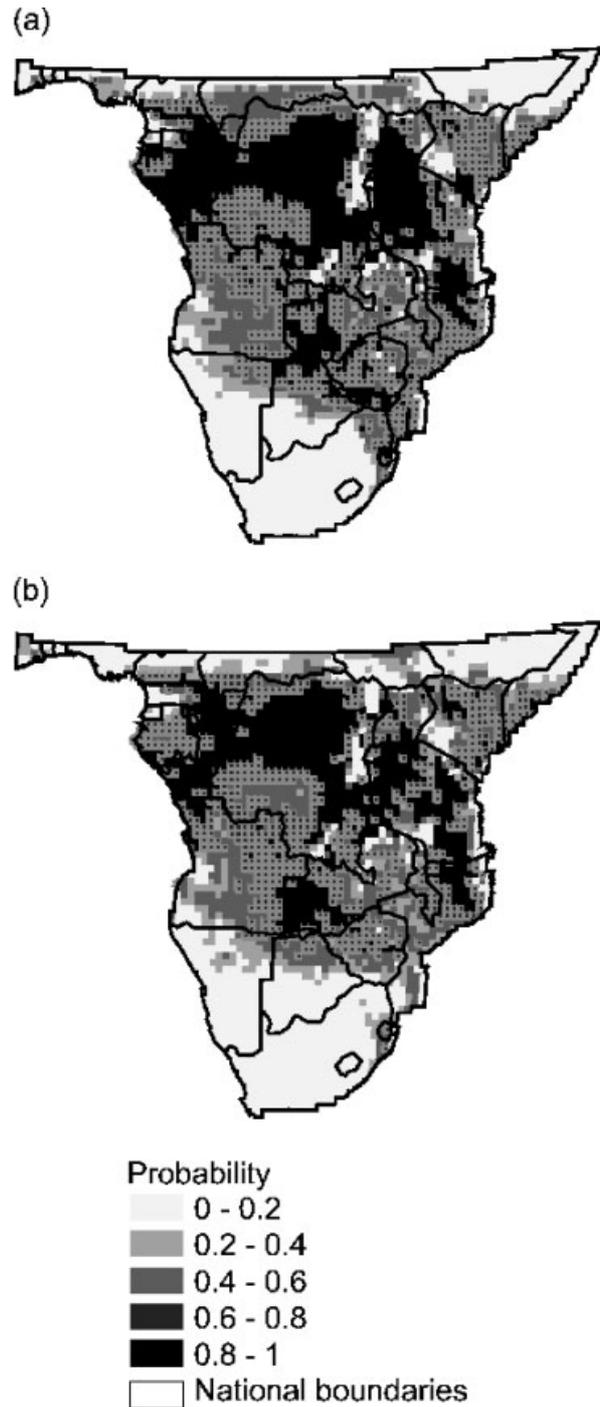


Figure 1. Predicted probability distribution of buffalo – *Syncerus caffer* obtained using species predictive modelling and DARAM climate fields (a) current (b) future.

current and future climate was done in S-PLUS (2000) while the analysis and production of current and future distribution maps were conducted in Arc View ESRI (2000).

2.7. Analyzing tick and host distribution range changes

The following analyses were performed to compare the current and future predicted distributions of ticks and hosts in response to simulated climate: (1) analysis of changes in the overall habitat suitability (probability

values) between the current and the future climates of *R. appendiculatus* and ten vertebrate hosts, (2) analysis of tick-host assemblage changes between the current and future predicted distributions, and (3) analysis of cattle-buffalo assemblage change. Predicted range changes were recorded and analysed and the expected implications of these changes for tick abundance and the prevalence of ECF were explored. Statistical significant tests were performed using Kolmogorov–Smirnov two-sample test StatSoft Inc. (2001).

2.8. Combined cattle and buffalo distribution changes

In order to determine a measure of climatic suitability of the grid cell for the two hosts, a combined probability of occurrence value for the two host species per grid cell was obtained. The probability product rule (Wadsworth, 1990) was used to combine the individual probabilities for the host species. This analysis was conducted on the ‘effective range’ of the species. The ‘effective range’ was taken as the areas where minimum conditions for the existence of a host were present and meant that all areas of zero probability of occurrence for host species were excluded from this analysis. This analysis was important in order to ascertain ECF transmission for the present and predicted future climate conditions.

3. Results

3.1. Future climate – DARLAM

The differences between the climates simulated by DARLAM for the period 2020s *versus* the 1990s, show that in January minimum and maximum temperatures will increase by more than 2 °C over most regions of sub-Saharan Africa (Figure 2) (Olwoch *et al.*, 2007). Many of the eastern regions are expected to become drier with an associated pattern of higher sea-level pressure, while the western subcontinent is expected to become wetter. July anomaly fields depict a cooler and wetter phenomenon in the central parts of the subcontinent.

3.2. *R. appendiculatus* predicted range alteration

A comparison of the predicted current and future ranges revealed contraction in climatic suitability for this tick species. There was a decrease in range of 54 grid cells which is equal to a reduction in area equivalent to 199 400 km². When the numbers of grid cells in various probability classes were compared, there was an increase in the number of grid cells in the lower probability especially between 0 and 20% probability class with a decrease in the number of grid cells in the upper probability classes (Table I) implying an overall decrease in climatic suitability for *R. appendiculatus* in the future predicted climate. The general reduction in *R. appendiculatus* habitat suitability may be linked to the predicted increase in dryer conditions in the Eastern parts of the continent, an area that is usually suitable for this tick species. Apart from the general range reduction, this

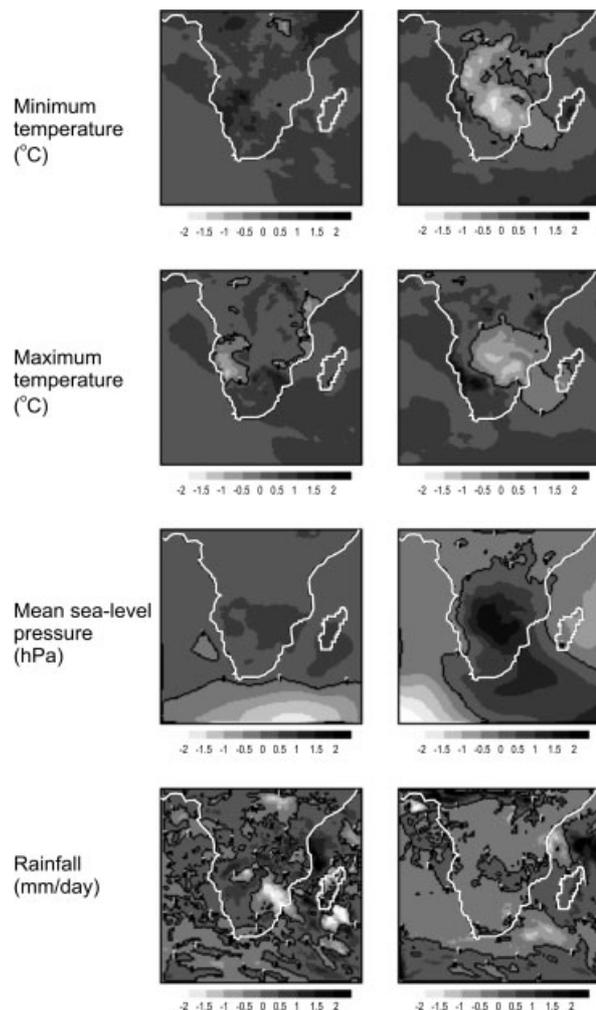


Figure 2. DARLAM climate fields.

Table I. Percentage change in the number of grid cells between the predicted current and future distributions in different probability classes for *R. appendiculatus*.

Probability class (%)	% change
0–20	188
20–40	20
40–60	21
60–80	–9
>80	–65

tick species also exhibited an east to west increase which reflected the tracing of DARLAMs predicted wetter July climatic conditions.

3.3. Broad scale range alterations in host species

The predicted current and future ranges of host species differ visibly and statistically (Kolmogorov–Smirnov; $p < 0.001$, $n = 3000$) for the following species: Burchell’s zebra, Waterbuck, Cape shrub hare, African savanna hare and buffalo (Figure 3). There were no significant differences between the predicted current and future range sizes of the other host species: Eland, Sable antelope, Impala

and Scrub hare. Further analysis of the predicted range changes between the current and future climates revealed that range contractions were the dominant range alterations for most of the host species. Ninety percent of the hosts are predicted to show range contractions ranging from 8 to 33%. This predicted range contraction is evident in both the hosts that support the development of all stages of *R. appendiculatus* and those that support only the larvae and nymphs. The only species predicted to show range expansion was the Cape hare, which gained 12% future suitability compared with its current range. The range expansion in this species may be related to its wide ecological tolerance/requirements. The Cape hare is known to occur primarily in open environments, including cultivated lands, from rich savannas to desert grasslands. It is also found in lightly wooded or bushed areas or mountain ranges. A comparison between areas occupied by *R. appendiculatus* and each of the hosts termed (tick-host assemblage) in the current and future predictions revealed surprising results in that the areas occupied by *R. appendiculatus* and each of the hosts increased substantially and some tick-host assemblages such as the buffalo and the tick, doubled in the future predicted distribution (Figure 4).

The predicted current combined range of the hosts intimately involved in ECF transmission (cattle and buffalo) is shown in Figure 5(a). High to moderate

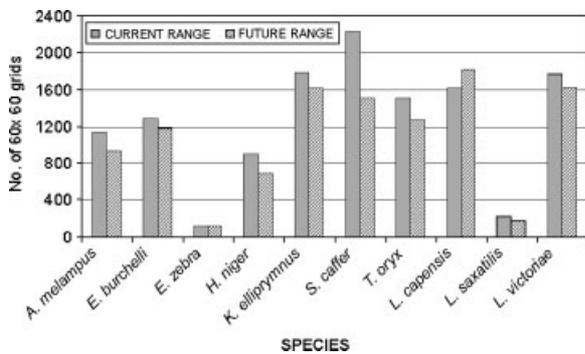


Figure 3. Predicted current and future range size (number of 60 × 60 grid cells) of all hosts using species predictive model and DARLAM climate fields.

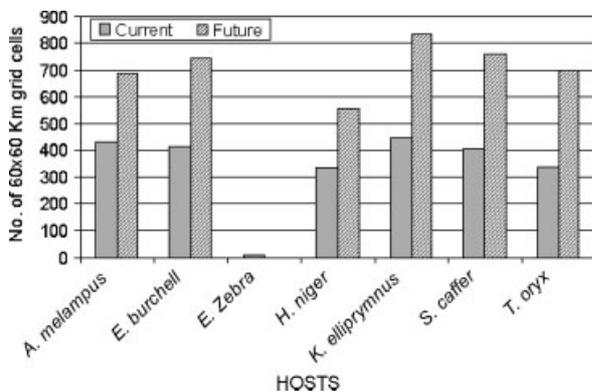


Figure 4. Predicted tick-host assemblages obtained using species predictive model and DARLAM climate fields.

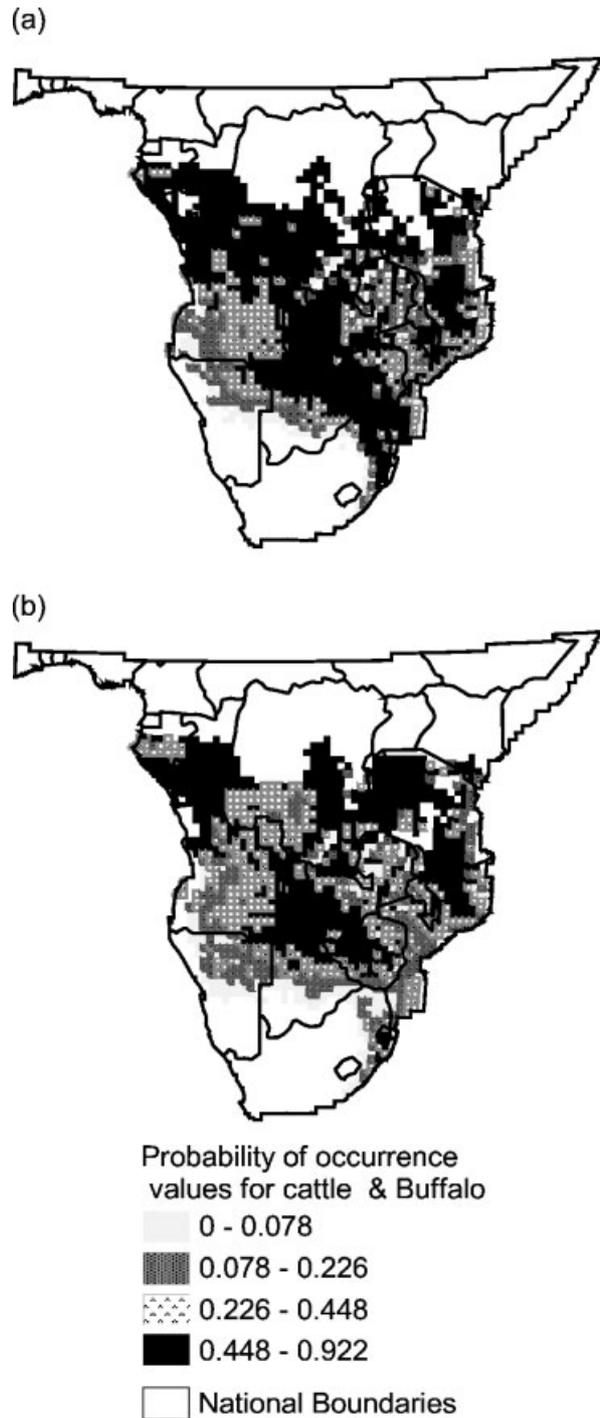


Figure 5. Predicted combined probability of the hosts that is intimately involved in ECF transmission obtained using species predictive modelling and DARLAM climate fields (a) current (b) future.

climate suitability is predicted in the Gabon, Congo, southern and eastern DRC, northern Angola, Tanzania, Mozambique, Zimbabwe, northern Botswana, and eastern Namibia. Under the predicted future climate, there is a notable reduction from 912 grid cells in the current climate to 412 grid cells in the future climate. Very high probabilities of future climatic suitability, however persist in the eastern DRC, north and central Tanzania and southwest Zambia (Figure 5(b)).

The differences in the maps of the current and future predicted climatic suitability for the total host assemblage revealed notable reductions in Congo, Gabon, the DRC, northern Tanzania, Angola, Botswana, Mozambique and in the north-eastern parts of South Africa. Expansions were predicted in a few areas including central Namibia, eastern DRC, south-eastern Angola, eastern Tanzania, and eastern parts of South Africa (Figure 6(a)). Similarly, differences in the current and future climatic suitability maps of the hosts intimately involved in ECF transmission (Figure 6(b)) revealed a general range reduction particularly in eastern and southern DRC, north-western Angola, northern Namibia, north-eastern parts of South Africa. With the predicted decrease in maximum temperatures and increase in rainfall in most of these areas one would have expected an increase in suitability. However

this is not the case because hosts' requirements are complex and may not at times be efficiently captured by a simple climate model. Increased host climatic suitability was however predicted for the eastern parts of Tanzania, Angola and Mozambique.

4. Discussion

4.1. Climate change, ticks and hosts distribution modelling

The precise part played by climate in determining the distribution of ticks, hosts and tick-borne diseases has not been adequately assessed and understanding the magnitude of the impacts of climate change on this system is even more challenging. This is due to practical difficulties in studying host distributions over time and the fact that both the distribution of ticks, hosts and diseases are a function of many other factors; social, economical and others. However, there is sufficient evidence to suggest that climate plays a vital part in determining their distribution. In this paper, the climatic suitability of one of Africa's most economically important ticks (*R. appendiculatus*) and ten animal species that act as its hosts and/or reservoirs to the pathogen (*T. parva*) have been provided through a modelling exercise. The resultant maps and data are intended to provide a risk profile for ECF in sub-Saharan Africa on the basis of one climate change scenario and also to demonstrate the impacts of climate change on these vertebrate hosts. Using the 'dilution effect' model, the implications of tick/host range alterations under a simulated climate on tick abundances and tick-borne disease infections are discussed.

A decline in the suitability of most areas in sub-Saharan Africa for the host species in response to a less suitable predicted future climate would likely translate into a loss of suitable habitat and possibly, at worst, species losses. This conclusion is on the basis of the existence of two major mechanisms of species loss: a decline of area and a decline in suitable habitat (Triantis *et al.*, 2003). Species losses alone would inevitably reduce the chances of ticks finding a suitable host and ultimately lead to a reduction in tick numbers. This is not valid to all species since generalists' species such as the Cape shrub hare increased their ranges and will likely flourish under conditions of climate change, providing adequate conditions for increased larvae population and ultimately higher tick numbers. Reduction in species diversity (predicted reduction in combined host probability) may increase the probability of ticks feeding on cattle, which is considered a competent reservoir for the parasite that causes ECF and lead to an ultimate increase in infection rate. This higher infection prevalence in cattle may also secondarily increase disease prevalence in wildlife because many of these emerging infections in wildlife are usually caused by a generalist pathogens that 'spills over' (Daszak *et al.*, 2000) from other species, often from domestic animals and to a certain extent from humans, especially in cases where the populations of other preferred hosts decline.

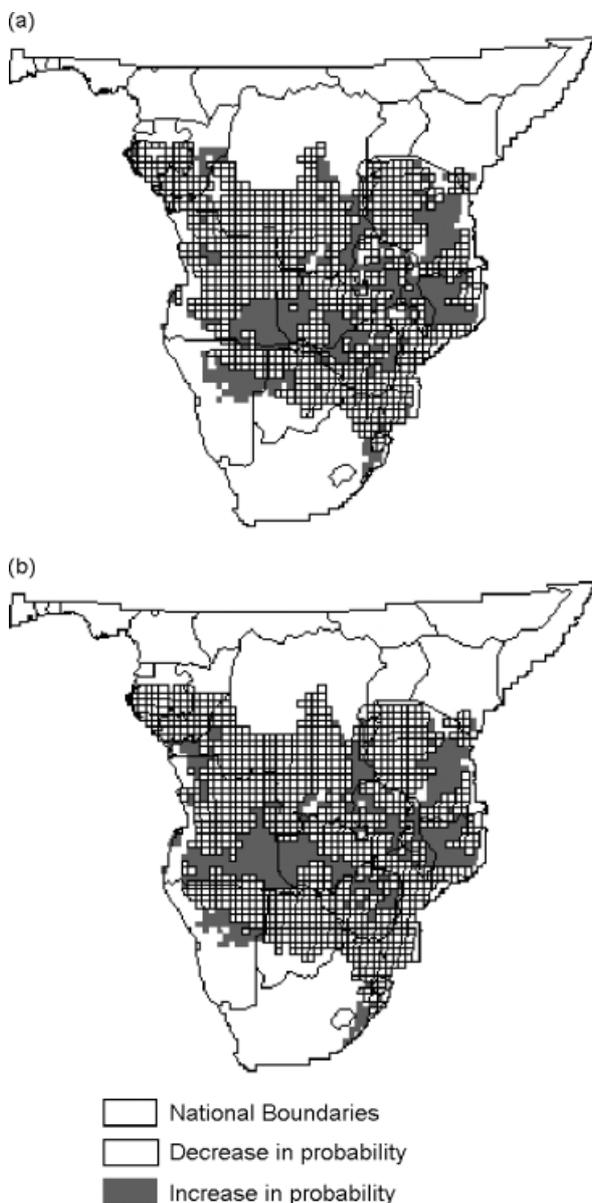


Figure 6. A difference between the predicted combined current and future hosts ranges (a) all hosts (b) cattle and buffalo.

The reduction in *R. appendiculatus* range predicted in this study may imply a reduction in tick numbers; however, an increase in tick-host assemblage ranges counteracts this effect resulting in a net increase in parasitic exposure to both domestic animals and wild animals. This could precipitate local wildlife extinction events in other host species. Moreover, the vulnerability of the tick-host-disease system to climate change could be further influenced by other climate change consequences such as land transformation, increased human population movement, cattle movements and other activities. These changes could place humans, their livestock and their pets into more direct contact with wild animals and the ticks that feed on them. Consequently, parasite life cycles that have been established between wild animals and ticks may be able to include livestock, pet animals and humans as well. For instance, the effect of forest fragmentation alone on the rodent hosts of Lyme disease has resulted in an increase in human exposure to the parasite (Allan *et al.*, 2003).

5. Conclusion and recommendations

The importance of biodiversity as a source of medicine or food supply has been well documented (Millennium Ecosystem Assessment (MA), 2003). The central role played by species diversity in the performance of ecosystem functions such as primary production and for resource extraction purposes is also rapidly emerging (Millennium Ecosystem Assessment (MA), 2005). However, the importance of biodiversity in the ecology of infectious diseases is still poorly understood. The inevitable links among climate change, the emergence of new diseases including HIV/AIDS, Lyme disease, Ebola, and Severe Acute Respiratory Syndrome (SARS) and the likely redistribution of old diseases such as malaria and TB and associated species losses are also poorly documented. Scant information exists regarding the effects of climate change on livestock diseases in Africa and even less information regarding the importance of host species in tick abundance and tick-borne disease prevalence exists. Yet for proper management of ticks and tick-borne disease, climate monitoring and the provision of early warning systems based on climate could offer promising results. Furthermore, regular monitoring of the reservoir hosts for infection is useful not only in devising appropriate tick-borne disease control programmes but also for the protection of the threatened wildlife species and for monitoring new feeding habits of parasites for probable emerging new zoonotic diseases.

This paper presents a first attempt at modelling the delicate interface between climate, ticks and vertebrate hosts. Though numerous factors at different spatial and temporal scales influence this complex system, an understanding of the part played by anticipated climate change is vital as one planning tool. Tick and host range changes demonstrated in response to climate are of concern both in terms of tick-borne disease control and in terms of conservation objectives. Since different areas in sub-Saharan

Africa are predicted to show varying range alterations, country specific concerted efforts such as facilitated range shifts, protection of their remaining habitats (Hannah *et al.*, 2005) and creation of corridors that will allow species to track climate change (Hannah *et al.*, 2002) are necessary to counteract these climate change impacts. As far as tick-borne diseases are concerned, regulation of cattle movement may be an important first step towards minimizing the contact zones between cattle and wild animals.

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