Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

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ABSTRACT

OLWOCH, J.M., VAN JAARSVELD, A.S., SCHOLTZ, C.H. & HORAK, I.G. 2007. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa. *Onderstepoort Journal of Veterinary Research*, 74:45–72

The suitability of present and future climates for 30 *Rhipicephalus* species in Africa are predicted using a simple climate envelope model as well as a Division of Atmospheric Research Limited-Area Model (DARLAM). DARLAM's predictions are compared with the mean outcome from two global circulation models. East Africa and South Africa are considered the most vulnerable regions on the continent to climate-induced changes in tick distributions and tick-borne diseases. More than 50% of the species examined show potential range expansion and more than 70% of this range expansion is found in economically important tick species. More than 20% of the species experienced range shifts of between 50 and 100%. There is also an increase in tick species richness in the south-western regions of the sub-continent. Actual range alterations due to climate change may be even greater since factors like land degradation and human population increase have not been included in this modelling process. However, these predictions are also subject to the effect that climate change may have on the hosts of the ticks, particularly those that favour a restricted range of hosts. Where possible, the anticipated biological implications of the predicted changes are explored.

Keywords: Climate change, *Rhipicephalus* species, sub-Saharan Africa, tick-borne disease

INTRODUCTION

The realization that species distributions are significantly influenced by climate has placed considerable emphasis on the need to acquire information concerning the ways in which the present distributions of organisms will be affected by climate change. In response to this challenge, the issue of vector distribution has recently received much attention. Numerous studies (Sutherst & Maywald 1985; Nix 1986; Perry, Lessard, Norval, Kundert & Kruska 1990; Norval, Perry & Young 1992; Rogers & Randolph 1993; Sutherst, Maywald & Skarratt 1995; Randolph & Rogers 1997; Estrada-Peña 1999; Rogers & Randolph 2000; Randolph 2001, 2002; Erasmus, Kshatriya, Mansell, Chown & Van Jaarsveld 2000; Erasmus, Van Jaarsveld, Chown, Kshatriya & Wessels 2002; Olwoch, Rautenbach, Erasmus, Engelbrecht & Van Jaarsveld 2003; Van Staden, Erasmus, Roux, Wingfield & Van Jaarsveld 2004; Thomas, Cameron, Green, Bakkenes, Beaumont, Collingham, Erasmus, Ferrierra, Grainger, Hannah, Hughes, Huntley, Van Jaarsveld, Midgley, Miles, Ortega-Huerta, Peterson,

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Accepted for publication 28 September 2006—Editor

Philips & Williams 2004) have attempted to predict the distribution of species based on the major environmental factors that would influence this.

This approach neither disregards the need for further detailed and comprehensive eco-physiological studies nor does it pretend to predict the future. What it does is define the role of climate as a factor in determining the potential for future vector establishment when all other elements are excluded (Sutherst 2003). This paper also accents the necessity of acquiring more detailed information concerning the biology and environmental sensitivities of each species in the light of likely climate change. In the absence of such information, relatively straightforward statistical methods that seek correlations between environmental factors and the presence of animals or plants are likely to remain the best pragmatic approach for exploring the expected future distributions of large numbers of species. This study focuses on climate induced changes likely to occur in the distribution of some species of an economically important African arthropod, namely the tick genus *Rhipicephalus*.

The intimate relationship between climate and the requirements of ticks for survival is well documented (Tukahirwa 1976; Rechav 1981, 1982; Short & Norval 1981; Minshull & Norval 1982; Norval, Walker & Colborne 1982; Dipeolu 1989; Perry *et al.* 1990; Norval *et al.* 1992; Okello-Onen, Tukahirwa, Perry, Rowlands, Nagda, Musisi, Heinonen, Mwayi & Opuda-Asibo 1999). This has led to several studies using climate as a means of predicting the distributions of African ticks (Rogers & Randolph 1993; Randolph 1993, 2001; Randolph & Rogers 1997; Norval, Sutherst, Kurki, Kerr & Gibson 1997; Cumming 2000a, b; Estrada-Peña 2001; Olwoch *et al.* 2003). Collectively the results obtained from these works, some of which used data garnered mainly from interpolated climate databases at 25 km resolution (Perry *et al.* 1990) or 6 x 6 km resolutions (Cumming 2000b), suggest that accurate predictions of tick distributions at different temporal and spatial scales should be feasible. This approach would be especially useful for predicting the distribution of species in poorly sampled species in poorly sampled regions of Africa.

The genus *Rhipicephalus* is the fourth largest in the Family Ixodidae (Walker, Keirans & Horak 2000), and there are 74 species currently recognized. It is essentially an African genus with approximately 63 species recorded only in the Afro-tropical region and ten species outside the region. One species, *Rhipicephalus evertsi evertsi* Dönitz, 1910, whose distribution was originally confined to the Afro-tropical region has now gained a foothold on the Arabian Peninsula and its distribution is expected to spread even further (Walker *et al.* 2000). Only 30 species are included in this paper. They are those whose ecological, life history strategies and climatic requirements are relatively well known and, as two distribution data sets have been used, the current distribution of these ticks are relatively well plotted. The way in which these distributions will be influenced by climate change is poorly documented and forms the essence of this paper.

The use of climate-matching models to predict tick distributions

One of the earliest climate matching approaches was CLIMEX, which calculates the climatic suitability of geographic regions for species using a temperature-dependent growth index moderated by four growth indices: hot, cold, dry and wet (Sutherst & Maywald 1985). The use of CLIMEX in northern Australia was considered a great success for predicting the distribution of the tick *Boophilus microplus* (Canestrini, 1887), and it was anticipated that this initial success could be translated into predicting distributions of African tick species. However, early studies tended to over-estimate the distribution of *B. microplus* across Africa, and the predicted high incidence of *Rhipicephalus appendiculatus* Neumann, 1901 in West Africa was at complete variance with the tick's absence in this region.

Moreover, when the distributions of *Amblyomma* spp. in Africa were modelled using CLIMEX, these were found to be dissimilar to their known distributions. These conflicting results led Norval, Perry, Meltzer, Kruska & Boothroyd (1994) to conclude that the predicted climatic suitability of regions for *Amblyomma hebraeum* Koch and *Amblyomma variegatum* Fabricius, 1794, is almost the opposite of the actual distribution of these ticks, both in Zimbabwe and in the rest of Africa (Norval, Perry, Gebreab & Lessard 1991; Norval *et al.* 1992).

BIOCLIM was the second climate-based approach employed to model tick distributions (Nix 1986; Norval *et al.* 1992). BIOCLIM generates 24 climatic attributes from which annual and seasonal mean conditions, extreme values and intra-year seasonality are derived, for each of a selection of geographic points throughout the distribution range of a tick species. Computer-selected thresholds and limits for each of the indices are matched across a geographical grid to predict potential species distribution. This model generally provided a better fit between the predicted and known distributions of *R.*

appendiculatus, although at a finer scale the match in some areas of the East African highlands was unsatisfactory (Norval *et al.* 1992). The climate database used was interpolated at an increased resolution (8 km), and this factor alone may explain the improved accuracy when compared to the earlier CLIMEX-based attempts. A subsequent logistic regression approach (Cumming 2000c), based on interpolated climate and elevation data for Africa with a resolution of 25 km (Hutchinson, Nix, MacMahon & Ord 1996) achieved even better accuracy. Such an approach, however, normally requires the existence of a training data set that includes presence and absence information (Estrada-Peña 2003). While it is relatively easy to ascertain where ticks have been collected, it is more difficult to confirm the reliability of surveys in which a tick species is cited as not present. Consequently the assumption that non-presence always implies absence may limit the application of this modelling approach (Estrada-Peña 2003).

The use of an Advanced Very High-Resolution Radiometer (AVHRR) mounted on the National Oceanic and Atmospheric Administration's (NOAA's) meteorological satellites was given preference in the 1990s. This instrument allowed the direct detection of environmental factors at an 8 km resolution (Lessard *et al.* 1990). The main predictor in this procedure is the satellite-derived maximum mean monthly Normalized Difference Vegetation Index (NDVI). However, this technique was reportedly very complicated when used to predict the distribution of *R. appendiculatus* (Kruska & Perry 1991). There are, however, initiatives to revive confidence in the NDVI approach as a predictive tool in research (Randolph 2002).

The present study used a single species distribution modelling procedure (Erasmus *et al.* 2000), originally developed by Jeffree & Jeffree (1994, 1996), for predicting species distribution patterns and for evaluating the relative performance of predicted future climate data sets. This model was subsequently modified to accept multivariate inputs to yield probability of presence maps for species (Erasmus *et al.* 2000). When used to predict the contemporary potential distribution of African ticks (Olwoch *et al.* 2003) the model achieved positive predictions of more than 70 % for the four tick species tested.

Climate data used for predicting African tick distributions

The principal sources of climate data for predictive distribution modelling are climate surfaces, generated by interpolating data sampled at varying intensities across a region. Consequently, differences between these climate surfaces can usually be attributed to spatial and temporal evenness of the data used for interpolation. Most modern interpolation techniques are pattern based and statistically incorporate horizontal as well as vertical (altitudinal) adjustments (Hutchinson 1989, 1991; Hutchinson & Gessler 1994). These climate surfaces are, however, relatively smooth because of extensive interpolation between low-resolution point observations.

Another source of climate data is Global Circulation Models (GCMs). These are coupled ocean-atmosphere models that provide three-dimensional simulations of the atmosphere. To date GCMs have produced climate data at a horizontal resolution that is generally too coarse for use in predictive species modelling (> 100 x 100 km grid point resolution), especially for species that are habitat specialists or that are influenced by fine-scale environmental gradients. Computational requirements usually preclude GCMs being run at meso-scale grid resolutions (10–100 km).

The present study used a Division of Atmospheric Research Limited Area Model (DARLAM) as the main climate data set. DARLAM is a potential alternative source of high-resolution climate data that involves the nesting of a high-resolution limited area model within a GCM over the area of interest (for review see McGregor 1997). The GCM supplies the limited area model with initial and boundary conditions. With a grid resolution of 10–100 km, the limited area model is able to simulate some of the meso-scale properties of the circulation model. This technique provides a viable fine scale alternative to the use of observed or interpolated climate surfaces or very coarse scale GCMs climate surfaces. The resolution attained by this dynamic modelling process is essentially limited by the computing power available to the modellers. The implication of using these datasets for predicting current tick distributions has been assessed by Olwoch *et al.* (2003). In this study, DARLAM's future predictions are compared with those obtained by using mean climates from two GCMs (CGCM and Centre for Climate System Research/National Institute for Environmental Studies [CCSR/NIES]).

MATERIALS AND METHODS

Study area

The study area covers sub-Saharan Africa (Fig. 1) and was divided into 3 000 grids cells of 60 x 60 km

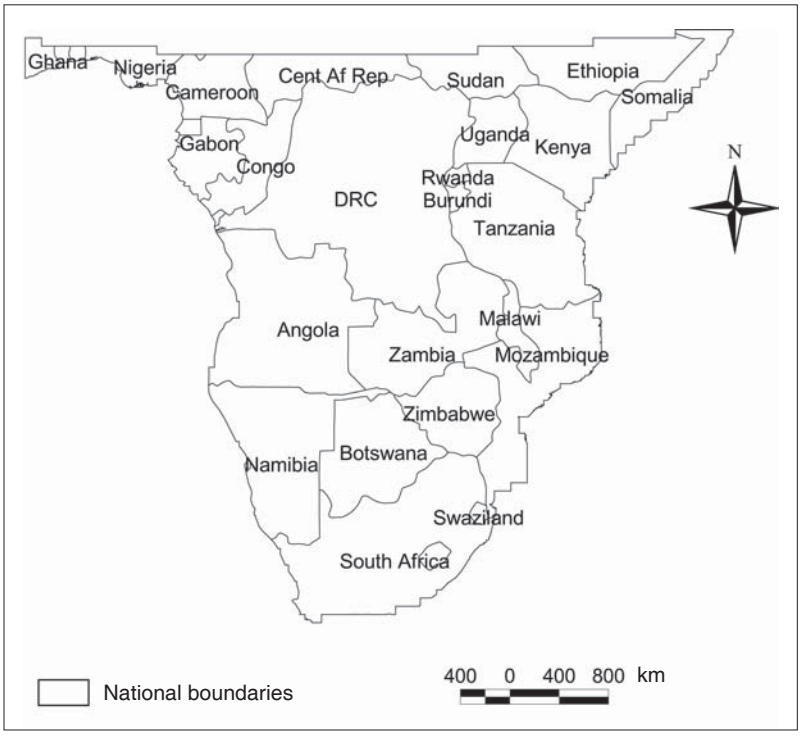

FIG. 1 Study area

resolution. This resolution was determined by the DARLAM climate data.

Tick data

Point localities of tick recoveries were obtained from Cumming (1999), who compiled the data that he used from various collections of ticks, and from recent collections made by one of us (I.G.H.). Combining data sets from different sources frequently compounds identification and distribution errors and for this reason data congruence with Walker *et al.* (2000), who provide well-illustrated distributions of *Rhipicephalus* species, was used to assess data quality in the final compiled dataset. Synonyms provided by the latter authors also solve the common dataset problem of referring to one species, but using different names, or referring to a group of species as a single species. The tick species selected for this study belong to the ixodid genus *Rhipicephalus*. Species point localities were assigned to particular 60 km x 60 km grid cells by means of a spatial intersect in ArcView GIS. A conservative estimate of the accuracy of these point localities is 0.2° (G.S. Cumming, personal communication 2003) and consequently this approximation is considered reasonable. The *Rhipicephalus* species selected are those whose distribution and life history strategies are relatively well known and it is our hope that these results will provide a baseline model for future modelling of other tick species.

Predictive species modelling

A simple climate envelope model was used to predict the future distribution of the focal species (Erasmus *et al.* 2000, 2002). The input data comprised 3000 grid cells of 60 x 60 km size populated with climate variables covering sub-Saharan Africa. Reliable presence records of the selected tick species and the present climate values at these locations were used to construct a climate envelope, using a principal components-type approach. This climate envelope represents the range of climates within which a particular tick is known to occur, and can be interpreted as the realized niche, as defined solely by climate. To arrive at a predicted distribution in 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 [see Erasmus *et al.* (2000, 2002) and Olwoch *et al.* (2003) for a more detailed explanation]. This approach was used as a standardized base for evaluating the relative performances of the DARLAM and the mean GCM climate data sets, and allows the creation of a probability surface of climate suitability for each species modelled.

DARLAM present and future climate data

The Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) developed the high-resolution limited-area model DARLAM for use in both short-term meso-scale atmospheric studies and longer-term climate simulation experiments (Walsh & McGregor 1995). In the present study ten separate 30-day simulations were performed for both January and July for separate 10-year periods. The periods selected are the 1990s and 2020. The simulations were performed at a horizontal grid resolution of 60 x 60 km using a domain of 100 x 100 grid points that cover sub-Saharan Africa. The monthly average of the ten simulations constitutes the model climatology for the month. The CSIRO Mark 2 GCM was used to force DARLAM at its lateral boundaries. The GCM was integrated for the period 1960–2100, with greenhouse gas forcing corresponding to the A_2 SRES (Special Report on Emission Scenario, issued by the Intergovernmental Panel on Climate Change) scenario.

Engelbrecht, Rautenbach, MacGregor & Katzfey (2002) illustrated that DARLAM is capable of simulating the regional characteristics of atmospheric variables such as near-surface temperature, low-level wind patterns and rainfall over sub-Saharan Africa with considerable detail. The model does, however, tend to overestimate total rainfall over regions with a steep topography. The DARLAM simulations were performed at the Laboratory for Research in Atmospheric Modelling (LRAM) at the University of Pretoria on a Pentium III workstation with two 550 MHz processors.

GCM future climate data

The GCM climate data used in this study were downloaded from the IPCC/DDC website. Through various stages in ArcView GIS, the original GCM data were processed to fit the 60 x 60 km resolution of DARLAM. The Canadian Global Coupled Model (CGCM2) was the first GCM climate used in this study. It is based on the earlier CGCM1, but with some improvements aimed at addressing shortcomings identified in the first version. In particular, the ocean mixing parameterization has been changed (Gent & McWilliams 1990), and following Flato & Hibler (1992) sea-ice dynamics has been included. The version of GCM2 used for control and doubled CO_2 experiments has ten vertical levels with the lowest prognostic level located at approximately 200 m above the surface. A description of CGCM2 and a comparison, relative to CGCM1, of its response to increasing greenhouse-gas forcing can be found in Flato & Boer (2001). The climate change projections used in this study are those from the newer IPCC SRES A2 scenario.

The second GCM model used was developed by the Center for Climate System Research/National Institute for Environmental Studies, (Japan) (CCSR/NIES) CGCM (Nozawa, Emori, Numaguti, Tsushima, Takemura, Nakajima, Abe-Ouchi & Kimoto 2001). This model is also based on Emission Scenarios (SRES) of the Intergovernmental Panel on Climate Change (IPCC). It is a Transient Coupled Ocean-Atmosphere Model, which was developed to investigate the direct and indirect climate impacts of the anthropogenic sulphate and carbonaceous aerosols in future projections of climate change. The data used here are from the A2 scenarios. Direct radiative forcing of the carbonaceous aerosols nearly nullifies that of the sulphate aerosols for all scenarios. Estimated total indirect radiative forcing is about –1.3 Wm-2 for the A1, B1, and B2 scenarios, and is about –2.0 Wm-2 for the A2 scenario in the latter half of the 21st Century. Global and annual averages of the surface air temperature increase for all scenarios because of the dominance of the radiative forcing of the increased CO_2. Global warming is decelerated with an increase in the anthropogenic sulphate and carbonaceous aerosols, because indirect forcing due to the aerosols has a significant cooling effect. Geographical distribution of the surface warming does not depend much on the scenarios. Cloud feedback becomes dominant in the latter half of the 21st Century, and this introduces further warming at the surface.

Predicting current and future distribution of *Rhipicephalus* species

The predicted current distributions were initially obtained using current climate predicted by DARLAM. This represents a useful comparison between predicted distributions and known records (see Olwoch *et al.* 2003). To obtain predicted future distributions the grid cells are populated with future climate variables. The predicted current distributions were obtained using the predictive species model (Erasmus *et al.* 2000) and six climate variables of current and future mean maximum temperature, mean minimum temperature and mean rainfall of January and July provided by DARLAM. The predicted future distributions were obtained by using both DARLAM and the mean GCM climates. The predictive modelling was executed in S-Plus (S-Plus 2000), while maps of the results were drawn in ArcView GIS. The resultant potential distribution maps represent the probability values of their suitability for ticks based on climate.

Analysis of predicted tick range changes

A number of analyses were performed to compare the predicted current and future distributions of ticks. These included:

(i) Analysis of species range expansion

(ii) An analysis of range contraction

(iii) Change in species richness pattern

(iv) Species range shifts

(v) An assessment of overlap between DARLAM and GCM predicted future distributions.

These range changes were initially analysed for the whole study area and subsequently, in some cases, on a regional basis. In the second analysis, ticks were grouped into the following regions depending on their principal regional distribution, namely East Africa, Central Africa and southern Africa, and a fourth group of ticks that were termed "general" ticks.

The East African tick species include *Rhipicephalus aquatilis* Walker, Keirans & Pegram, 1993, *Rhipicephalus armatus* Pocock, 1900, *Rhipicephalus bequaerti* Zumpt, 1949, *Rhipicephalus carnivoralis* Walker, 1966, *Rhipicephalus humeralis* Rondelli, 1926, *Rhipicephalus kochi* Dönitz, 1905, *Rhipicephalus maculatus* Neumann, 1901, *Rhipicephalus muehlensi* Zumpt, 1943, *Rhipicephalus planus* Neumann, 1907 and *Rhipicephalus pulchellus* Gerstäcker, 1873.

The Central African species include *Rhipicephalus complanatus* Neumann, 1911, *Rhipicephalus compositus* Neumann, 1897, *Rhipicephalus dux* Dönitz, 1910, *Rhipicephalus longus* Neumann, 1907, *Rhipicephalus lunulatus* Neumann, 1907, *Rhipicephalus masseyi* Nuttall & Warburton, 1908, *Rhipicephalus punctatus* Warburton, 1912, *Rhipicephalus senegalensis* Koch, 1844, *Rhipicephalus supertritus* Neumann, 1907 and *Rhipicephalus ziemanni* Neumann, 1904.

The southern African species include ticks of the *Rhipicephalus capensis* group (*Rhipicephalus capensis* Koch, 1844; *Rhipicephalus follis* Dönitz, 1910 and *Rhipicephalus gertrudae* Feldman-Muhsam, 1960), *Rhipicephalus distinctus* Bedford, 1932, *Rhipicephalus exopthalmos* Keirans & Walker, 1993, *Rhipicephalus oculatus* Neumann, 1901, *Rhipicephalus zambeziensis* Walker, Norval & Corwin, 1981 and the subspecies *Rhipicephalus evertsi mimeticus* Dönitz, 1910.

There are also species that have wide ranging distributions that overlap in various regions of Africa. These species, termed "general" ticks include *R. appendiculatus, R. evertsi evertsi* Neumann, 1897, *Rhipicephalus pravus* Dönitz, 1910 and *Rhipicephalus simus* Koch, 1844. The above groupings are presented to facilitate interpretation of the current findings and do not imply that the ticks placed in particular geographical regions are restricted to these areas, but rather localise their distribution with extensions into neighbouring regions.

Range expansion and contraction

In order to obtain range changes in terms of contractions or expansions, predicted current or future distributions were first obtained. The predicted current or future distributions were taken as the number of grid cells in which the probability of occurrence is equal to or greater than 50 %. The difference in the number of grid cells between the predicted *present distribution* (DP) and predicted *future distribution* (DF) constitutes *distribution range change* (DC). These range changes may either represent contractions or expansions. We initially performed this analysis on a sub-Saharan scale and later on a regional scale in order to establish which regions in Africa would experience greater changes in predicted tick distribution ranges (current and future) and therefore appear more vulnerable to climate change. We analysed the differences between the predicted distributions using the Kolmogorov-Smirnoff two-sample test. Furthermore, we divided the ticks into economically important and unimportant species. A comparison of range changes between the current and future predictions was performed on this latter grouping to assess which of the two groups is more vulnerable to climate change.

In all the above analyses we assessed the proportion of species that experienced expanded or contracted range changes and the degree of the predicted expansion/contraction.

Analysis of change in species richness pattern and degree of range shifts

Species richness patterns were calculated as the number of species in the predicted current or future distribution per grid cell following Erasmus *et al.* (2002). This analysis was performed for the whole of sub-Saharan Africa. Range shifts were calculated as the number of additional grid cells in the predicted future distribution as a proportion of the current predicted distribution. We used the current predicted distribution instead of current known records because most regions in Africa are poorly sampled.

Comparing predicted future distributions of ticks based on climates simulated by DARLAM and GCM

The accuracy of any climate model is as good as the initial conditions that are used to configure it. Since there is no climate model that provides an accurate projection of the future, it seemed prudent to use the results from more than one climate model in this study. A comparison was therefore made to assess the differences between the predicted future climate suitability for tick species using a regional climate provided by DARLAM and a mean of two GCMs described above. The analysis was performed on a sub-Saharan scale and also on a regional scale. We assessed the degree of proportional overlap between the predicted current distribution and the predicted future distribution (DARLAM and GCM) by means of the proportional overlap method (Prendergast, Quinn, Lawton, Eversham & Gibbons 1993; Reyers, Van Jaarsveld & Krüger 2000). In this case the proportional overlap was calculated as Nc/Ns where Nc is the number of common grid cells between a pair of areas under comparison and Ns is the number of grid cells containing data for both groups or the maximum number of overlapping grid cells possible.

RESULTS

Model Validation was not performed in this study because the same climate envelope model had previously been subjected to rigorous evaluation using presence-absence data resulting from a coordinated and systematic survey effort. Erasmus *et al.* (2002) used the distribution records of 34 bird species and tested performance of the model using receiver operator characteristic analyses (Fielding & Bell 1997). The model performed significantly better than a random model with no discriminatory ability. It also accurately predicted the complete known distributions for 24 of the 34 bird species, using a 20% sub-sample of the known records (Erasmus *et al.* 2002). This satisfactory documented performance of the model and the relatively good predictions that were obtained when it was used to predict the current distributions of four African ticks (Olwoch *et al.* 2003) are sufficient reasons to consider the model adequate for the present study.

Future climate—DARLAM

The climatological anomalies for the 2020s vs the 1990s as predicted by DARLAM are depicted in Fig. 2. January minimum and maximum temperatures are simulated to increase by more than 2 °C over certain regions of sub-Saharan Africa. Many of the eastern regions are expected to become drier with an associated pattern of higher sea-level pressure, whilst the western subcontinent is expected to be-

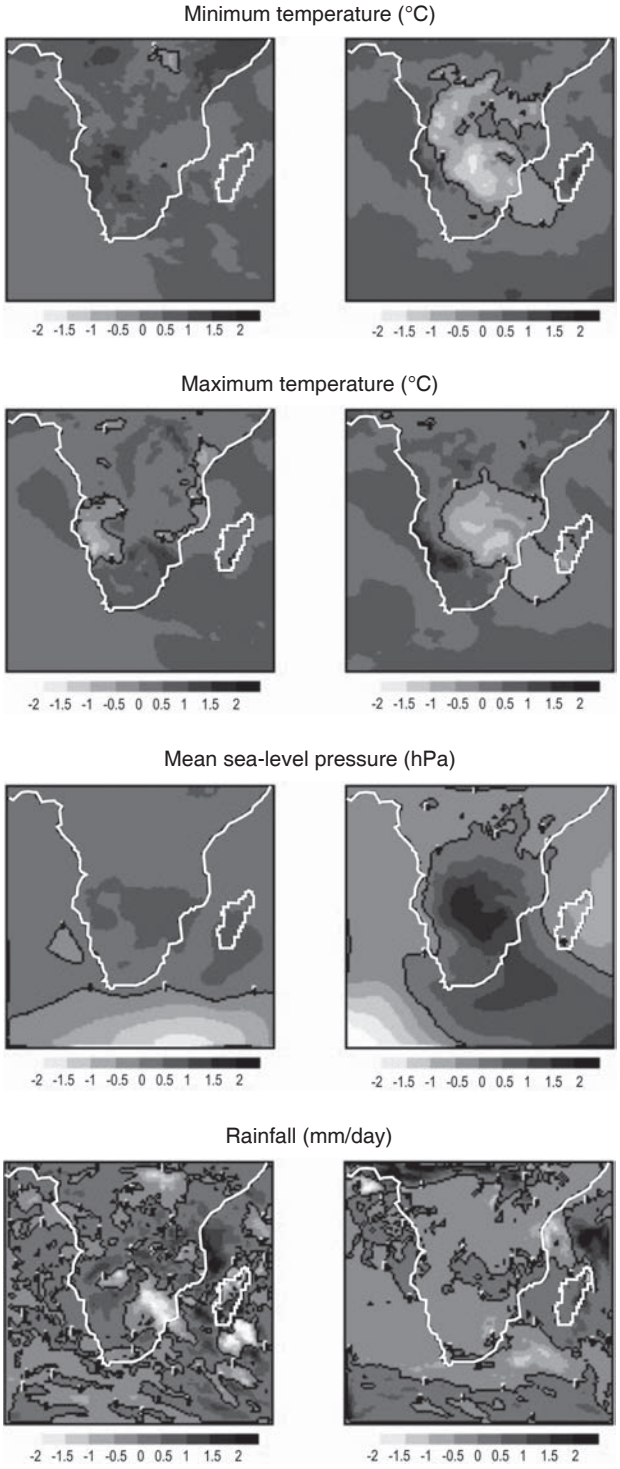

FIG. 2 DARLAM's climatological anomalies for the 2020s v. 1990s

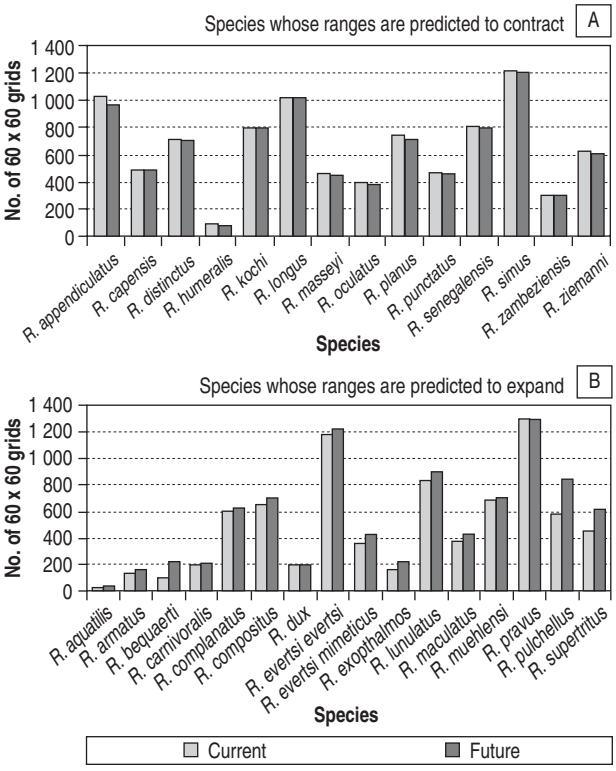

FIG. 3 *Rhipicephalus* species in sub-Saharan Africa that are predicted to show (A) range size contraction and (B) range size expansion

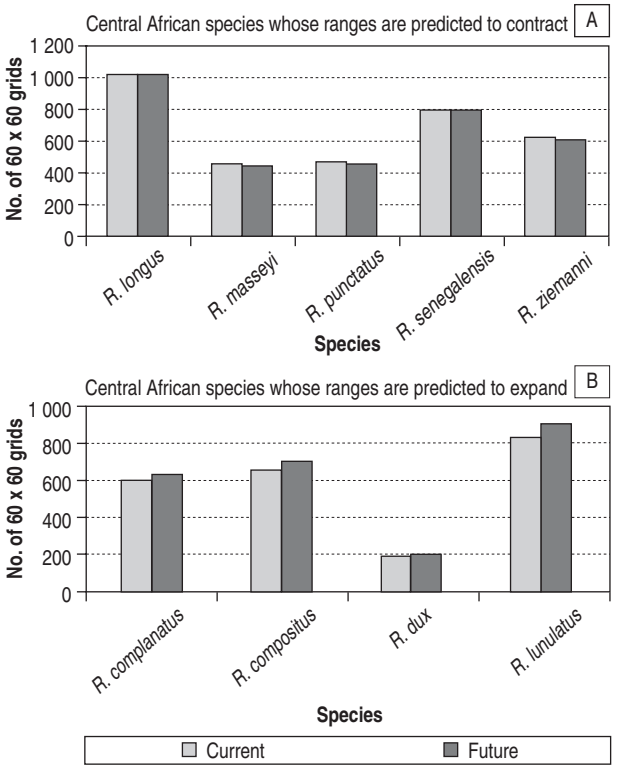

FIG. 4 *Rhipicephalus* species in Central Africa that are predicted to show (A) range size contraction and (B) range size expansion

come wetter. An interesting feature of the July anomaly fields is that parts of the central subcontinent are simulated to become cooler and wetter.

Species distribution changes

Broad scale range changes (Fig. 3A, B)

The predicted current and future distributions of the selected *Rhipicephalus* spp. using DARLAM are provided in figures 10–39. On a sub-Saharan scale, the ranges of 46% of the tick species, namely *R. appendiculatus, R. capensis* group*, R. distinctus, R. humeralis, R. kochi, R. longus, R. masseyi, R. oculatus, R. planus, R. punctatus, R. senegalensis, R. simus, R. zambeziensis and R. ziemanni* are predicted to contract. The ranges of 54% of the species, namely *R. aquatilis, R. armatus, R. bequaerti, R. carnivoralis, R. complanatus, R. compositus, R. dux, R. evertsi evertsi, R. evertsi mimeticus, R. exopthalmos, R. lunulatus, R. maculatus, R. muehlensi, R. pravus, R. pulchellus* and *R. supertritus* are predicted to expand over the same period (Fig. 3A, B). These results translate into an area expansion of 3 502 800 km^2 (12%) in total tick range with a total reduction of 640 800 km^2 (2%).

Central African species (Fig. 4A, B, 16,17, 19, 25, 26, 28, 34, 35 and 39)

Fifty-five percent of species in central Africa are predicted to show range reductions (*R. longus, R. masseyi, R. punctatus, R. senegalensis* and *R. ziemanni*) while 45% (*R. complanatus*, *R. compositus*, *R. dux* and *R. lunulatus*) are predicted to show range expansions. Although the ranges of the majority of tick species are predicted to contract, the total area of contraction is only 19%, while the total area of expansion by the remaining species is 81%. The tick species predicted to expand its range most in this region is *R. lunulatus* with a total expansion of 252 000 km^2.

East African species (Fig. 5A, B, 11, 12, 13, 15, 23, 24, 27, 29, 31 and 33)

In East Africa 30% of the species (*R. humeralis, R. kochi* and *R. planus*) are predicted to show range contractions, while 70% (*R. aquatilis, R. armatus, R. bequaerti, R. carnivoralis R. maculatus, R. muehlensi* and *R. pulchellus*) are predicted to show range expansions. This translates into a total expansion of 1 760 400 km^2 (91%) with a mere 169 200 km^2 (9%) reduction in total area. The predicted greater expansions are mainly attributable to *R. bequaerti* which

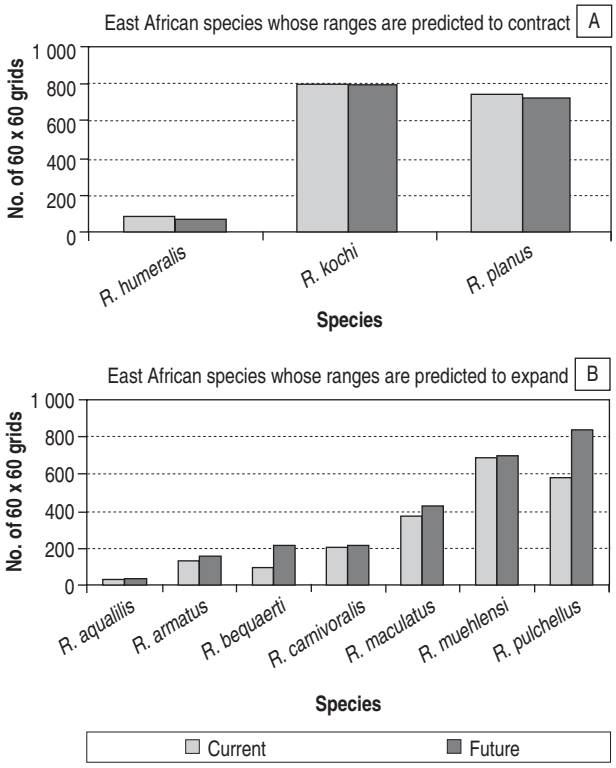

FIG. 5 *Rhipicephalus* species in East Africa that are predicted to show (A) range size contraction and (B) range size expansion

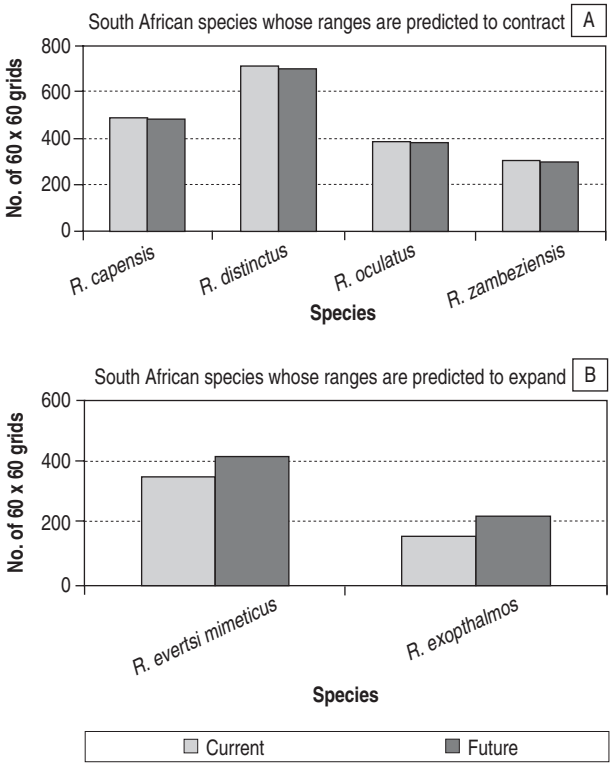

FIG. 6 *Rhipicephalus* species in southern Africa that are predicted to show (A) range size contraction and (B) range size expansion

more than doubles its present range and *R. pulchellus,* which is predicted to expand its range by some 921 600 km^2 (49 %).

Southern African species (Fig. 6A, B, 14, 18, 21, 22, 30 and 38)

In southern Africa some 66 % (*R. capensis* group*, R. distinctus, R. oculatus* and *R. zambeziensis)* of the tick species are predicted to contract their ranges. Although only 33 % (*R. evertsi mimeticus* and *R. exopthalmos*) of the ticks are predicted to expand their current ranges, the total range expansion is 439 200 km^2 (23 %) while the total range reduction is only 64 800 km^2 (1 %). Most of the expansion in this region is attributable to *R. evertsi mimeticus*.

"General" tick species (Fig. 7A, B, 10, 20, 32 and 36)

The "general" ticks are those *Rhipicephalus* species that are widely distributed with current distributions overlapping within various geographical regions of the subcontinent. This does not necessarily mean that these species are not specialists with regard to their ecological requirements, e.g. *R. appendiculatus* is confined to parts of eastern, central and southeastern Africa (Walker *et al.* 2000). It is a species of significant economic importance in Africa because it transmits *Theileria parva,* the cause of East Coast fever (ECF), which is a major cause of cattle mortality and also causes considerable production losses in cattle in most African countries (Okello-Onen *et al.* 1999). The only tick species predicted to contract its range in this group is *R. appendiculatus*, which is predicted to contract its range by 212 400 km^2 (5 %). The ranges of 75 % of the ticks in this category, namely *R. evertsi evertsi, R. pravus* and *R. simus* are predicted to expand. The total range expansion in this region is equivalent to 864 000 km^2 (7 %). This expansion is mainly associated with *R. simus*, which is predicted to expand its range by 601 200 km^2 (70 %).

Changes in species richness patterns and range shifts

The future climate predicted by DARLAM will alter the species richness distribution pattern of African *Rhipicephalus*. Compared to the current pattern (Fig. 8A) the predicted pattern is spatially different and broader (Fig. 8B) with encroachment of ticks into new regions. These regions, which include An-

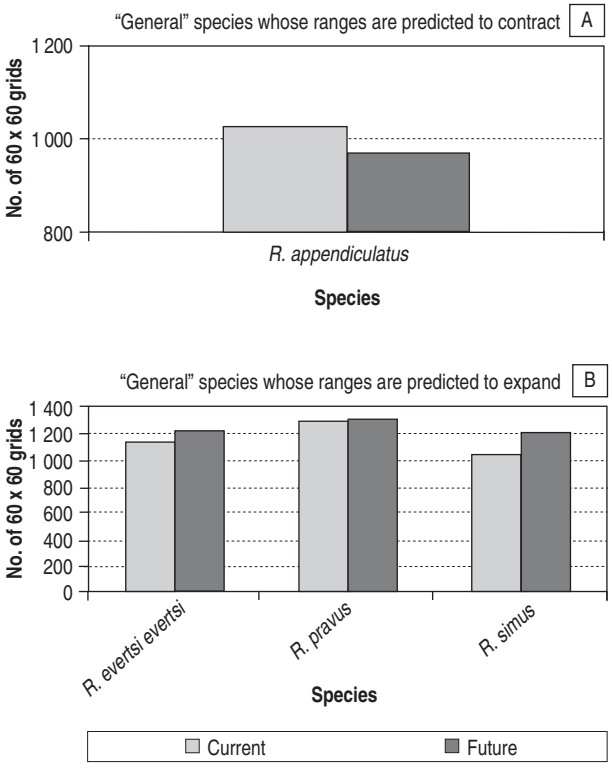

FIG. 7 *Rhipicephalus* species in the "General" ticks that are predicted to show (A) range size contraction and (B) range expansion

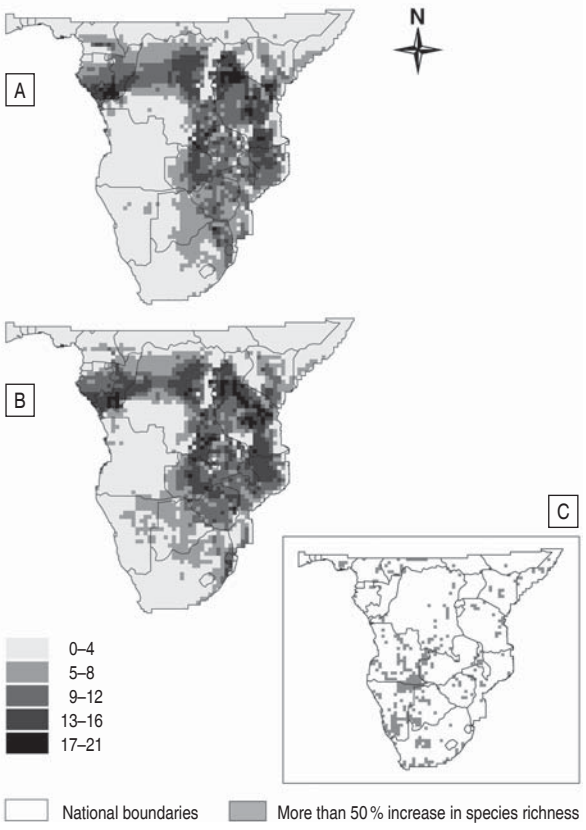

FIG. 8 Species richness pattern of *Rhipicephalus* species in sub-Saharan Africa: (A) current; (B) future; and (C) areas with more than 50 % increase

gola, Namibia, Botswana and the Northern Cape Province of South Africa, are forecast to experience a more than 50 % increase in tick species richness (Fig. 8C). This could be related to increased rainfall in these regions, rendering the south-western regions of sub-Saharan Africa more suitable for ticks. The general west-east shift in species ranges reported by Erasmus *et al.* (2002) is not supported in this study on ticks, in which varying degrees of shift in different directions appears to be the emergent pattern for this taxon. Analysis of range shifts further indicates that 80 % of species show less than a 50 % range shift, while 20 % of species show a range displacement of more than a 100 %. The latter species are mainly those that populate the western arid regions of Africa (Fig. 8).

Species range changes and tick-borne disease implications

Thirty percent of the ticks included in this study are classified as economically important because they are vectors of diseases of domestic livestock or other animals (Table 1). Although *R. appendiculatus*, the principal *Rhipicephalus* vector of disease in Africa shows range contraction, the remaining vectors are responsible for 52 % of the predicted range expansion under future climate conditions. The non-vector species are responsible for 48 % of future tick range expansions.

Predicted future distributions using DARLAM and GCM climate data

The predictions of future climate suitability for ticks when DARLAM is used are generally more extensive than those generated when using the combined GCM climates. With the exception of four species (*R. compositus, R. evertsi mimeticus, R. exopthalmos* and *R. oculatus*), and the *R. capensis* group, DARLAM predicts wider ranges of climatic suitability than the combined GCM climate surfaces. DARLAM's total predictions are 31 % broader than the GCMs. The average difference in the range sizes predicted for DARLAM and GCM is 511 200 km^2. Statistically there is no significant difference between the predictions by DARLAM and GCM using a Kolmogorov-Smirnov test ($P > 0.1$, $n = 30$). However, when the climate data simulated by DARLAM and GCM are analysed for statistical significance, there

TABLE 1 *Rhipicephalus* spp. and the diseases with which they or the toxins they produce are associated

Disease and causal agents	Animal affected	Vectors
East Coast fever (*Theileria parva*)	Cattle	*R. appendiculatus* *R. zambeziensis*
Tick toxicosis	Cattle	*R. appendiculatus*
Corridor disease or Buffalo disease (*Theileria parva*)	Cattle, buffalo	*R. appendiculatus* *R. zambeziensis*
Gall sickness (*Anaplasma marginale*)	Cattle	*R. evertsi evertsi* *R. simus*
Equine biliary fever or equine piloplasmosis (*Babesia caballi*, *Theileria equi*)	Horses, mules, donkeys	*R. evertsi evertsi*
Spring lamb paralysis	Lambs, calves	*R. evertsi evertsi*
Canine biliary fever or canine tick fever (*Babesia canis)*, rickettsiosis (*Ehlichia canis)*	Dogs	*R. sanguineus*
Paralysis	Sheep, lambs, calves	*R. lunulatus*
Nairobi sheep disease (*Bunyaviridae*)	Sheep	*R. pulchellus*

TABLE 2 Proportional overlaps between pairs of grid cells between the predicted ranges from DARLAM and the ranges predicted using mean values for two GCMs

"General" tick species	DARLAM 2030	GCM 2030	Common grids	Proportional overlap value (%)
R. appendiculatus	969	858	476	55
R. evertsi evertsi	1 220	945	611	65
R. pravus	1 300	868	621	29
R. simus	1 209	858	597	60
East Africa				
R. aquatilis	33	17	5	29
R. armatus	153	116	29	25
R. bequaerti	215	40	11	28
R. carnivoralis	205	111	67	60
R. humeralis	79	33	12	55
R. kochi	797	491	326	29
R. maculatus	425	173	98	56
R. muehlensi	699	678	315	67
R. planus	719	413	278	55
R. pulchellus	841	217	179	25
Central Africa				
R. complanatus	626	595	400	67
R. compositus	**699**	**737***	443	60
R. dux	201	192	77	40
R. longus	1 020	990	642	25
R. lunulatus	897	518	308	28
R. masseyi	450	338	202	60
R. punctatus	458	440	262	28
R. senegalensis	803	622	415	56
R. ziemanni	611	558	352	72
South Africa				
R. capensis group	**485**	**547***	309	56
R. distinctus	707	352	254	72
R. evertsi mimeticus	**423**	**577***	49	49
R. exopthalmos	**212**	**236***	116	15
R. oculatus	**386**	**434***	293	49
R. zambeziensis	299	226	169	60

Bold* = GCM predictions wider than those of DARLAM

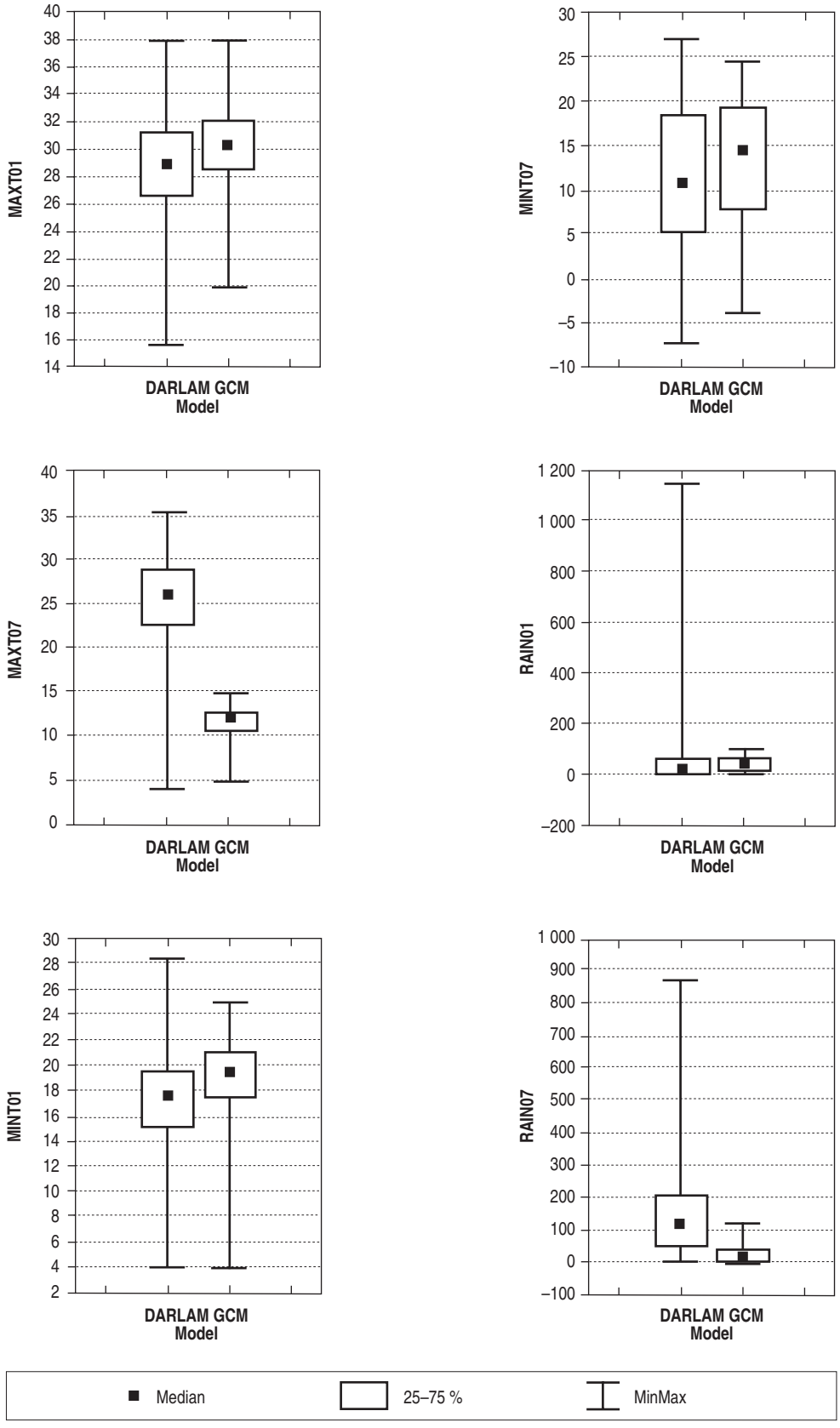

FIG. 9 Box plots based on the Kolmogorov-Smirnov test that compared climate predicted by DARLAM and a combined GCM

FIG. 10–39 Predicted probability distribution of *Rhipicephalus* species using DARLAM and GCM future climates: (A) DARLAM; (B) GCM

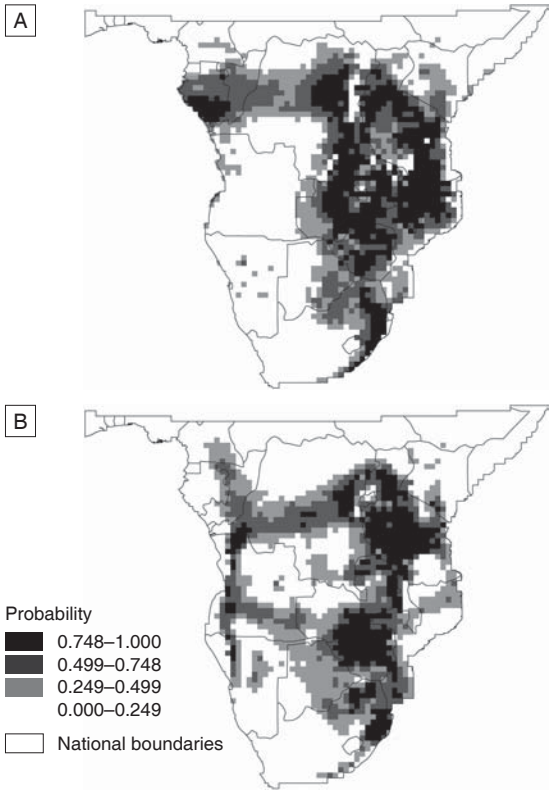

FIG. 10 *R. appendiculatus*

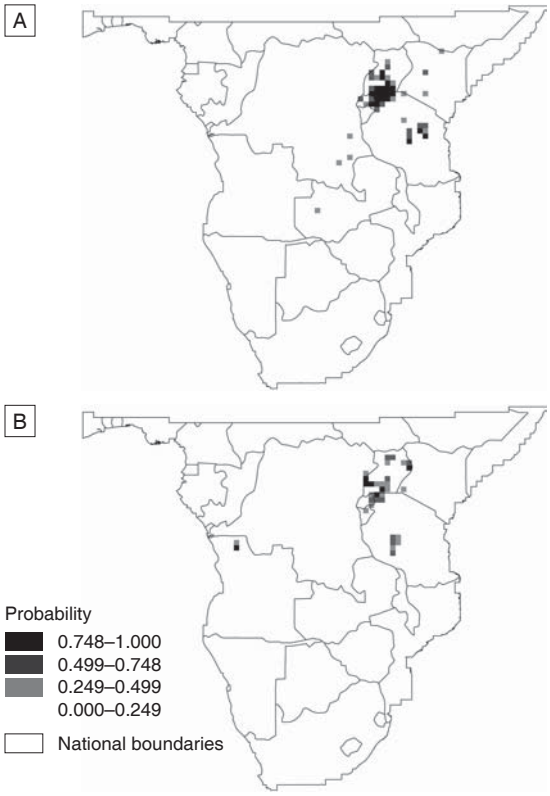

FIG. 11 *R. aquatilis*

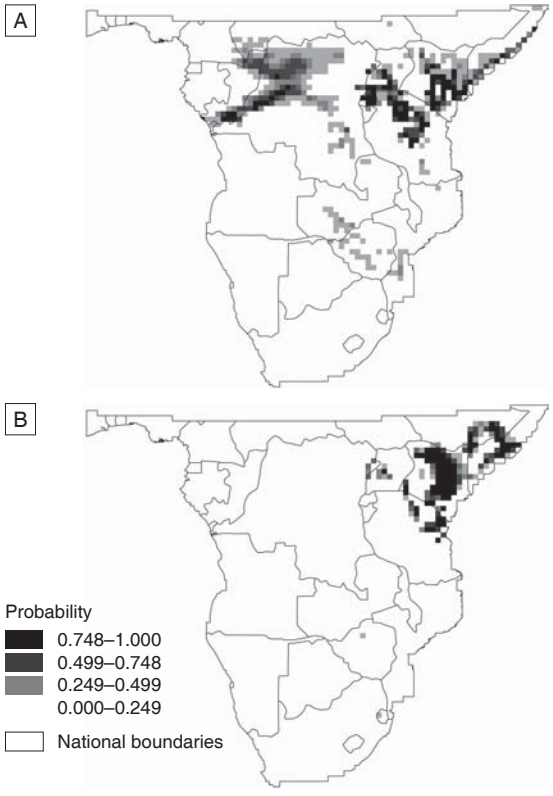

FIG. 12 *R. armatus*

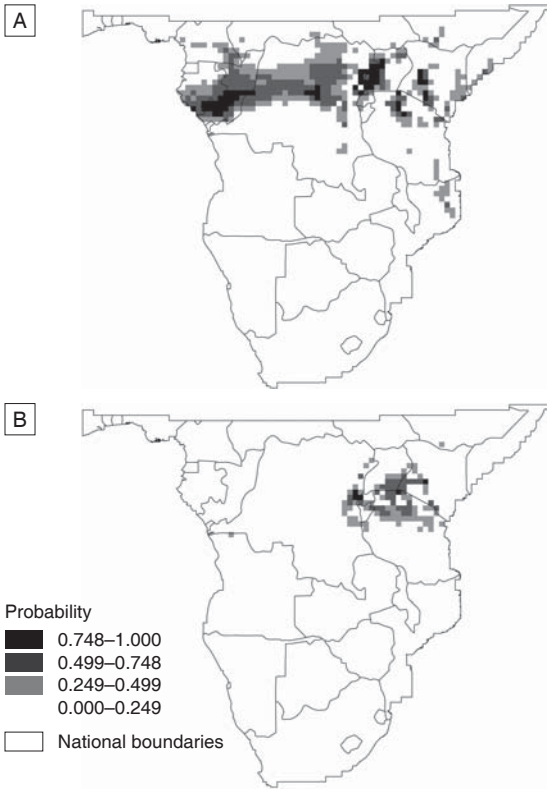

FIG. 13 *R. bequaerti*

FIG. 10–39 *Continued*

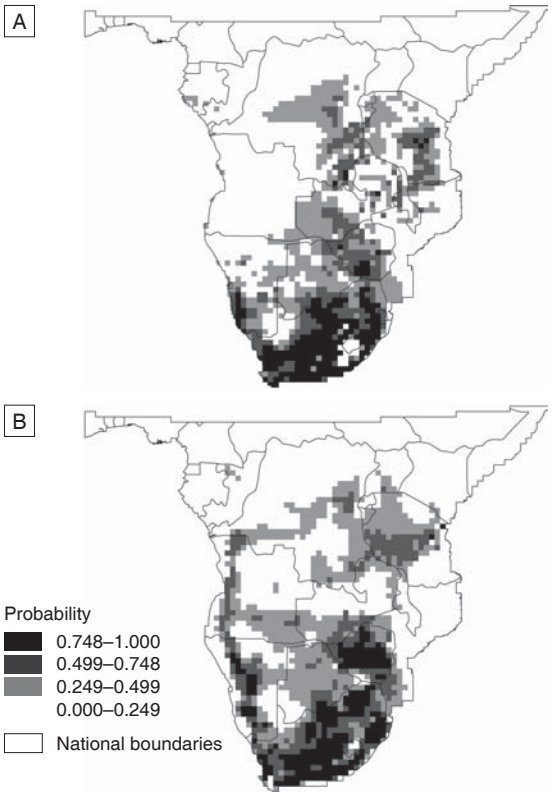

FIG. 14 *R. capensis* group

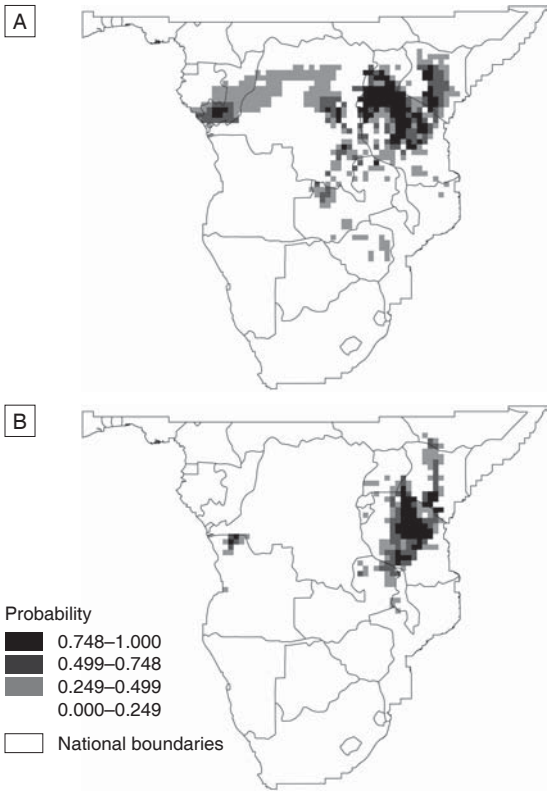

FIG. 15 *R. carnivoralis*

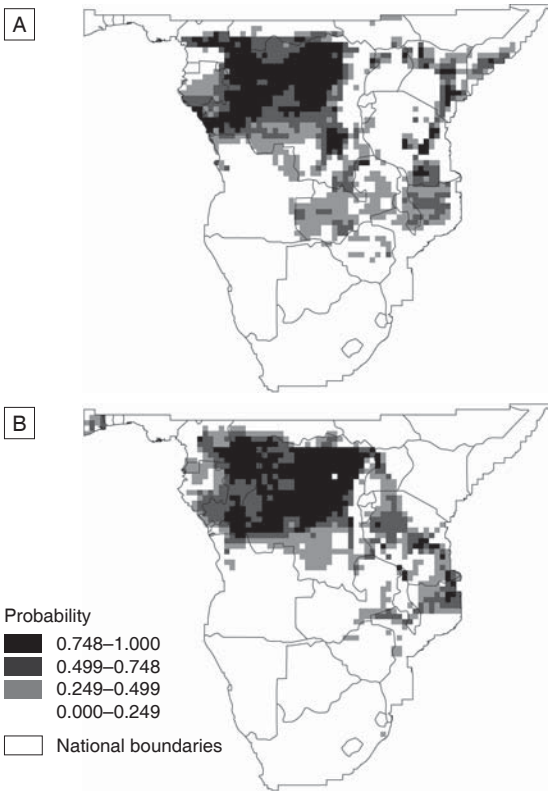

FIG. 16 *R. complanatus*

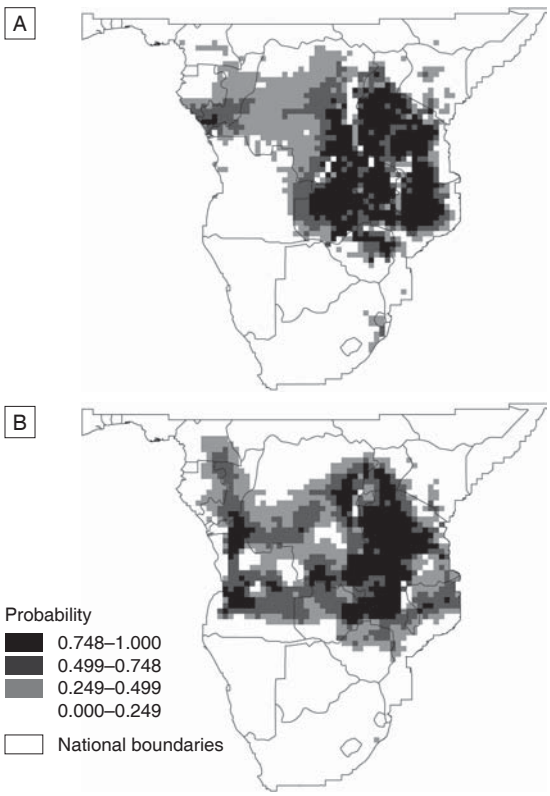

FIG. 17 *R. compositus*