The known distribution and ecological preferences of the tick subgenus *Boophilus* (Acari: Ixodidae) in Africa and Latin America

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Abstract. A compilation of the known distribution of *Boophilus* ticks in Africa and Latin America is presented, together with details on climate preferences. *B. annulatus* is recorded mainly in the western part of a strip from the equator to parallel 20° N. It associates with woodlands and forests (lowland rain forest and secondary grassland). This species is also present in the Mediterranean region, associated to woodland and open areas. *B. decoloratus* extends southern to parallel 20° N, in woodland with montane vegetation and Zambezian miombo; some records have been collected in the highveld grassland. *B. geigyi* is mainly collected in the western range of a stripe extending between parallels 5° N and 18° N, associated with Sudanian woodland, lowland rain forest with secondary grassland and woodland. Confirmed records of *microplus* in Africa are restricted to Malagasy region and south and eastern Africa, being predominant in the Zambezian miombo, deciduous forest with secondary grassland, and woodland. In Latin America, *microplus* is abundant in the Mesoamerican corridor to Venezuela and Colombia, and southern in Brazil and Argentina. The tick is mainly associated to the biomes of Chaco and Pampas in Argentina, the North-central moist Andes, the Atlantic forest (southern range) and the moist Meso-American vegetation (northern range). Most collections of *B. annulatus* and *B. geigyi* came from areas where winter minimum temperature is above 15 °C, maximum temperatures remain between 33 and 36 °C and maximum rainfall is recorded between June and September. *B. decoloratus* and African *B. microplus* are recorded in sites with low temperatures in May–September. Minimum temperature requirements are similar for both *B. decoloratus* and African *B. microplus*, and both are around 4 °C less than the value recorded for collections of Latin-American *B. microplus*. The rainfall pattern observed for *decoloratus* shows a minimum in May and June. The requirements of total rainfall are highest for *B. microplus* in Latin America, while records of African *B. microplus* are concentrated in areas of low rainfall between May and October, and high rainfall between November and March (low rainfall in the same period for *B. decoloratus*). Statistical analysis revealed the existence of populations (demes) with ecologically different requirements within each tick species. Both *B. annulatus* and *B. decoloratus* showed many different demes clearly associated

to defined areas. The collections of Latin American *B. microplus* are very homogeneous according climate preferences and well separated from the African counterpart.

Introduction

Boophilids are some of the most important tick species in the world from an economical point of view. Each of the five *Boophilus* species has a one-host life cycle that may be completed in 3–4 weeks and results in heavy tick burden (Walker et al. 2003). *B. microplus*, considered the most important parasite of livestock in the world, has been introduced from the bovid- and cervid-inhabited forests of the Indian region to many areas of tropical and subtropical Asia, northeastern Australia, Madagascar, coastal lowlands of southeastern Africa to the equator, and much of South and Central America, Mexico and the Caribbean. *B. annulatus*, original from the former southern USSR, the Near and Middle East, and the Mediterranean area, was introduced with livestock of the early Spanish colonialists into northeastern Mexico but has not spread into Central America. *B. microplus* and *B. annulatus* were eradicated from the USA after a long, costly control program, and constant surveillance is maintained to prevent its reintroduction (George 1987). *B. decoloratus*, which ranges from southern Africa to the Sahara, is being replaced in the eastern and southeastern part of this area by *B. microplus*. This seems to be caused by the shorter life cycle of *microplus*, as well as the tendency to assortative mating and more successful feeding on cattle and is cause of much concern in the area, because the expansion of *microplus*-transmitted pathogens (Tonnesen et al. 2004). In more humid West African zones, *B. annulatus* mixes with or is totally replaced by *B. geigyi*. However, no competition has been reported between these species, as little is known from the life cycle of *B. geigyi*. *B. annulatus* further extends into eastern Africa, as a line southern to the limits of Sahara desert. The only boophilid restricted to sheep and goats (and occasionally horses) is *B. kohlsi* of Syria, Iraq, Israel, Jordan, western Saudi Arabia, and the Yemen. *Boophilus microplus* is an experimental vector of *Theileria equi*, and this tick and *B. annulatus* are major vectors of *Babesia bigemina*, *Babesia bovis*, and *Anaplasma marginale*. *B. decoloratus* is an efficient vector of *B. bigemina* and *A. marginale* but does not transmit *B. bovis*. This tick apparently does not transmit *T. equi*, but it is an experimental vector of *A. marginale* to cattle. Recent studies of the taxonomy of the group, using molecular taxonomy methodologies, have proposed a radical change placing the five species in the genus *Boophilus* in the genus *Rhipicephalus* (Murrell et al. 2000; Beati and Keirans 2001). Horak et al. (2002) proposed to *Boophilus* as a subgeneric epithet. Throughout this paper, however, *Boophilus* will be used as not final decision about the taxonomic status of these five species has been officially approved. It should be noted that this does not imply a position about the systematics of the boophilids, but only a way to refer to the ticks included in this study.

Ecological niches delineate the set of conditions under which species can maintain populations in the long-term. Individuals living outside the niche

conditions do not replace themselves. There is a wide theoretical treatment of the features of the ecological niche (Holt 1996; Holt and Gomulkiewicz 1996) that clarifies the relationships between ecological niche, geographic distributions and evolutionary dynamics. These studies suggest that, in general, long-term natural selection pressures will maintain the ecological niche without substantial modification. This reasoning supports the idea that species ecological niche represents long-term stable constraints on geographic distributional potential. The fundamental niche can be viewed as the set of conditions and resources that allow a given organism to survive and reproduce in the absence of biotic interactions. An understanding of the fundamental niche can provide us with greater insight into the causes of distribution and abundance. This is a solid foundation for exploring the role of biotic interactions and to extrapolate with greater confidence the adaptation to novel circumstances such as climate change and species introductions. We present in this study data about the known distribution of *Boophilus* ticks in Africa and Latin America. Populations of ticks of the same species are detected, as groups of ticks supporting different climate conditions. An overview of the climate preferences as calculated among the statistically detected populations of ticks is also presented, as a mechanistic approach to study the climatic component as driving force of the distributions of ticks in the subgenus.

Material and methods

The basis for the current study has been the huge compilation of data on the distribution of ticks in Africa, Latin America and the Caribbean performed by the authors (ICTTD 2004). In that preliminary study, published records from ticks as well as data from collections in scientific institutions were compiled, edited by local experts, and mapped to latitude and longitude coordinates. Data from a previous compilation by Cumming (1999) have been also edited to remove inaccurate references or misdeterminations, and added to the database. The compilation on which this paper is based is thus the largest database on the recorded distribution of *Boophilus* ticks. Some data have not been used, as follows. *B. kohlsi* was not included in the original compilation because its importance for domestic animals is unknown (Walker et al. 2003). Our current knowledge about the distribution of *Boophilus* ticks in areas of Asia is still fragmentary. This study is intended to provide a complete review in the areas were these ticks are present, so it has been considered better to not incorporate the records from Asia. Data on *B. microplus* in Australia are selective for the area known to be infested and we lack adequate references (geographical data) to collection sites. Therefore, only records from Africa and the Neotropics have been included. Records from *B. annulatus* in the Americas have been also omitted, as the presence of this taxon in the region is scattered. Furthermore, early records from both *B. microplus* and *B. annulatus* in USA have been avoided, as it is difficult to ascribed these records to the climate at the time they

were collected. For the whole study, records lacking an adequate geographical reference were not included.

This database of tick records has been checked against a spatially and temporally extensive gridded climate data set that extends between 1950 and 1999. The data set of world climate was built by New et al. (1999) and was developed by interpolating observations taken at meteorological stations, corrected with the altitude. This is a gridded data set that contains monthly records of temperature (mean, minimum and maximum) and precipitation (monthly total) at a resolution of 10 km. Other than these basic monthly variables, we compiled a further set of 19 variables that are herein called yearly variables. Those explain much of the variability in the year, and contribute to further homogenize observations. The yearly variables are 1: Annual Mean Temperature, 2: Mean Diurnal Range (Mean of monthly (max temp − min temp)), 3: Isothermality (2/7 * 100), 4: Temperature Seasonality (standard deviation * 100), 5: Max Temperature of Warmest Month, 6: Min Temperature of Coldest Month, 7: Temperature Annual Range (5–6), 8: Mean Temperature of Wettest Quarter, 9: Mean Temperature of Driest Quarter, 10: Mean Temperature of Warmest Quarter, 11: Mean Temperature of Coldest Quarter, 12: Annual Precipitation, 13: Precipitation of Wettest Month, 14: Precipitation of Driest Month, 15: Precipitation Seasonality (Coefficient of Variation), 16: Precipitation of Wettest Quarter, 17: Precipitation of Driest Quarter, 18: Precipitation of Warmest Quarter, 19: Precipitation of Coldest Quarter.

We extracted both monthly and yearly variables for each tick record. Care was taken to associate each tick record with the climate at the time the collection was done, using the averaged climate values of the year of capture (as included in the tick database) and the 5 previous years. This procedure provided every tick record with the climate to which it has been associated and avoided the bias derived from the connection of the tick record with uncommon climate values. No attempts were done to obtain also climate features from sites where no data on *Boophilus* ticks was available to compare with climate values for ticks records. The mapping of ticks as absent in sites where only other species were collected may introduce a potentially dangerous bias in the actual distribution of a species. For each tick species, we obtained the range of values (mean ± SD) for every monthly and yearly variable.

The complete set of records for each species was separated in demes, representing populations of ticks within the same species collected in statistically different ecologically zones. This part of the study is intended to know if populations with statistically different climate preferences exist in diverse geographic areas and to understand the ecological niche relationships within demes of each species. This point has major implications in predictive mapping, as projecting algorithms are commonly evaluated over populations covering relatively large areas. It has been already demonstrated that habitat classification (presence/absence) accuracy for *Glossina* spp. became further accurate by subdividing the habitat into ecological zones prior to performing discriminant analysis (Robinson 1998). However, we cannot use only climate to sub-

divide the habitat into significantly different zones, as the climate conditions under which the ticks have been collected would be correlated with these climatically different regions. The subdivision of the area into statistically different zones based solely on climate would provide automatically different tick populations. For this purpose, we selected a set of remotely sensed images with monthly information of Normalized Derived Vegetation Index (NDVI, which is linearly uncorrelated with climate) and performed an unsupervised classification of the habitat in Africa (including the Mediterranean part) and Latin America. The procedure provided with an assemblage of NDVI-based habitat categories, whose NDVI value are statistically homogeneous within each category, and different for zones between separate categories. Records of each species as collected into each vegetation category were initially treated as separate demes. A cluster analysis was performed in using the climate data associated to every tick record to understand the relationships of the species as clusters in the *n*-dimensional space of the climate variables. To avoid bias in the estimation, vegetation categories representing less than 5% of the captures of the species were avoided in further analysis. This procedure allows a direct comparison of the climate requirements by the strict definition of the space of variables as requirements or each species. Special attention was paid to *B. decoloratus* and the African records of *B. microplus*. The spread of *B. microplus* in Africa has been already reported for some parts of the continent, replacing *B. decoloratus* in parts where the climate is suitable for the invader (Tonnesen et al. 2004). This procedure will provide with information about the ecological space occupied by both species, and the degree of ecological plasticity of *B. microplus* in Africa.

Results

Figures 1 to 3 display the zones where boophilid ticks have been collected, with information about the vegetation categories separated according NDVI. *B. annulatus* is present in a relatively wide strip extending from the equator to parallel 20° N, being predominant in the western part of this stripe (Figure 1a). The species is also present north of the Sahara, with most collections in Morocco and Tunisia, and scattered in zones of Egypt, Libya and Algeria. It associates with two main types of vegetation dynamics, namely one which remains at low NDVI values for much of the year (Mediterranean region and first zone south of Sahara desert) and one with clear increase in NDVI after July–August, coinciding with the rainy season. The species has been collected as associated mainly with woodlands (Sudanian and undifferentiated woodland) and forests (lowland rain forest and secondary grassland). *B. decoloratus* extends into much of Africa, southern to parallel 20° N with some isolated records northern to Sahara. These records appear to be accidental importations. It is associated with several vegetation categories, all of them but two being characterized by a prominent decrease of NDVI values between May and
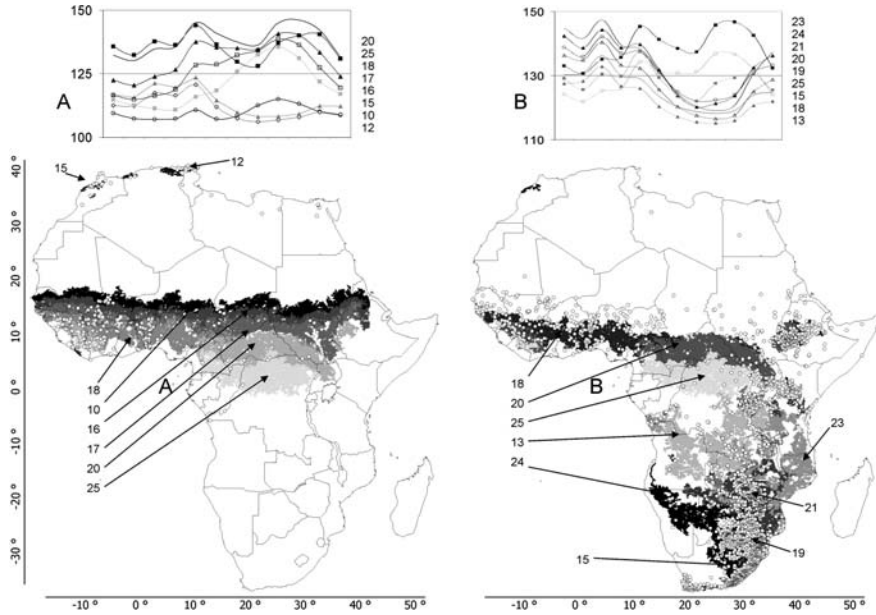
Figure 1. Distribution range of *B. annulatus* (a) and *B. decoloratus* (b) in Africa. Dots show the confirmed records of these ticks. Areas in different shades of grey are the statistically different vegetation areas (according to monthly NDVI values) determined by unsupervised classification, to which records of ticks are associated. Areas where less than 5% of tick records of each species have been collected are not shown. Maps include reference to Latitude and Longitude (bars below and lateral). Upper to each map is a chart with the monthly profile of NDVI values for each vegetation zone, in a range from 0 to 256. Each number as associated with areas in the map and charts are the vegetation classes as recorded by unsupervised classification of NDVI values.

September and then an increase in the last part of the year. The two remaining regions, located at the northern portion of its distribution range (arrows in Figure 1b), are characterized by high values of NDVI, with an increase after September. *B. decoloratus* has been collected associated to a variety of biomes. It is a tick of woodland, mainly undifferentiated woodland with montane vegetation and Zambezian miombo. Some records have been collected in the highveld grassland. *B. geigyi* is mainly collected in the western range of a narrow stripe extending between parallels 5° N and 18° N, although the vegetation zones where the tick has been found extend well into eastern Africa. All these categories of vegetation are characterized by relatively high NDVI values with a small decrease in July–August. The exceptions are the zones in the northern range of distribution (mainly in central Mali) where NDVI values are low in the first months of the year. The species is mainly associated to Sudanian woodland, lowland rain forest with secondary grassland and undifferentiated woodland. A significant proportion of captures has been collected associated to wetter types of lowland forests. Confirmed records of *B. microplus* in Africa are restricted to Malagasy region and south-eastern Africa, in areas mainly
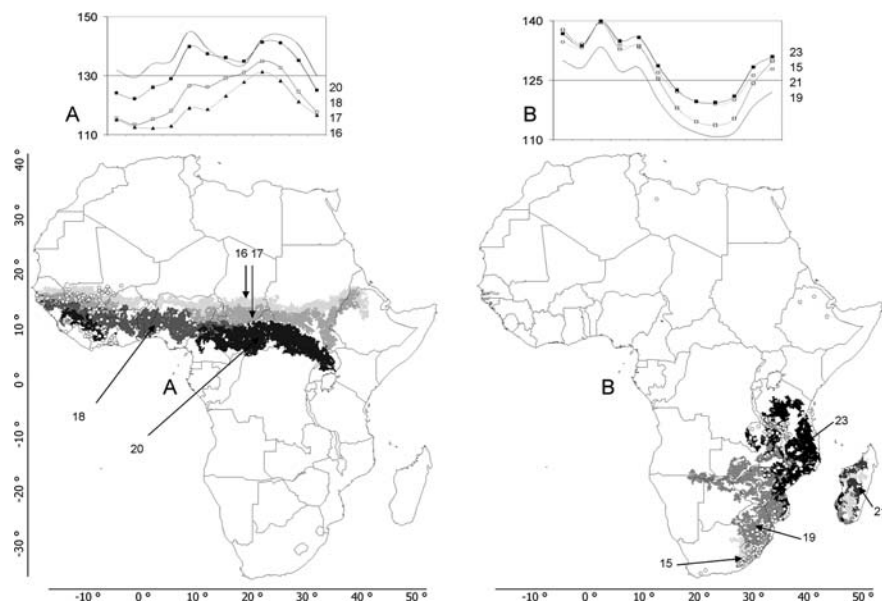
Figure 2. Distribution range of *B. geigyi* (a) and *B. microplus* (b) in Africa. Dots show the confirmed records of these ticks. Areas in different shades of grey are the statistically different vegetation areas (according to monthly NDVI values) determined by unsupervised classification, to which records of ticks are associated. Areas where less than 5% of tick records of each species have been collected are not shown. Maps include reference to Latitude and Longitude (bars below and lateral). Upper to each map is a chart with the monthly profile of NDVI values for each vegetation zone, in a range from 0 to 256. Each number as associated with areas in the map and charts are the vegetation classes as recorded by unsupervised classification of NDVI values.

characterized by very low NDVI values between July and October, coincident with a dry season (see below) while keeping high the rest of the year. While the vegetation zones where *B. microplus* has been found in Africa are easily characterized by NDVI values, they fall within a wide range of biomes, the tick being predominant in the Zambezian miombo, the mosaic of dry deciduous forest with secondary grassland, and the undifferentiated woodland. In Latin America, *B. microplus* has a bipolar distribution, being abundant in the Mesoamerican corridor to Venezuela and Colombia, and southern in Brazil and Argentina. Scatter records occur in the Amazonian region, probably as result of importations. *B. microplus* occupies two types of vegetative areas according to NDVI values: the first is located in the northern portion of its distribution range, and characterized by relatively high, slightly variable NDVI values through the year, while the second is located in its southern distribution range, and characterized by very high NDVI values with a sharp decrease in mid-winter (August–October). The tick is mainly associated to the biomes of Chaco and Pampas regions in Argentina, together with the North-central moist Andes, and the Atlantic forest (southern range) and the moist Meso-American vegetation (northern range).
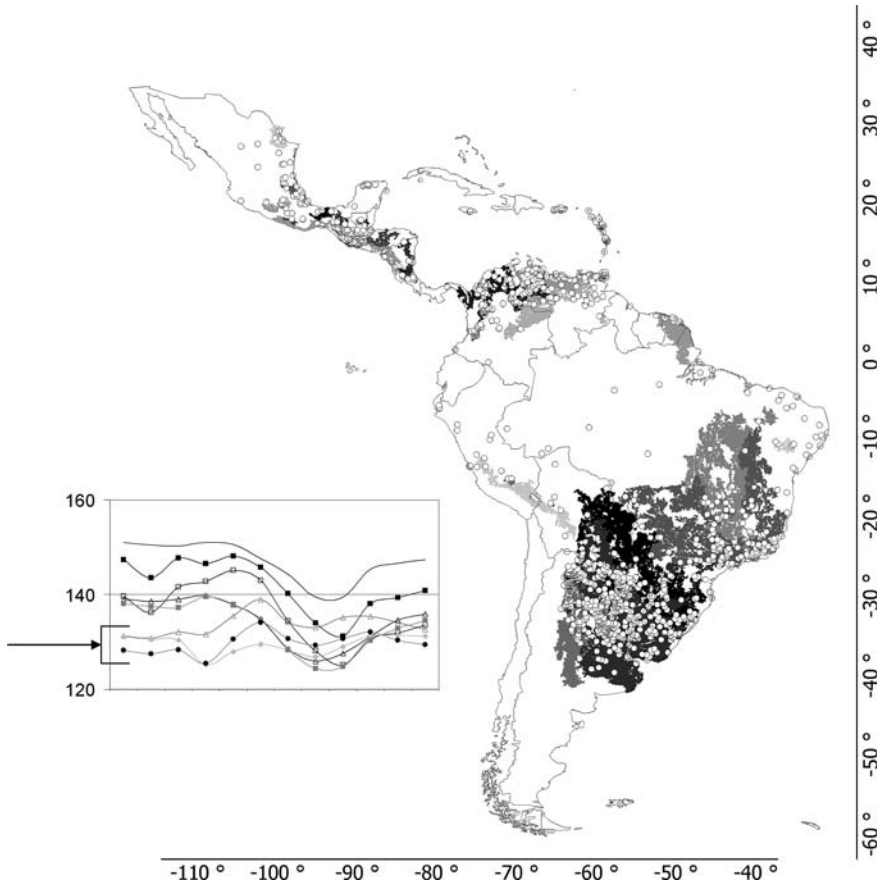
Figure 3. Distribution range of *B. microplus* in Latin America. Dots show the confirmed records of these ticks. The tick is present in many parts of the Caribbean, but adequate coordinates to these records are lacking. Areas in different shades of grey are the statistically different vegetation areas (according to monthly NDVI values) determined by unsupervised classification, to which records of ticks are associated. Areas where less than 5% of tick records of each species have been collected are not shown. Map includes reference to Latitude and Longitude (bars below and lateral). Upper to the map is a chart with the monthly profile of NDVI values for each pictured vegetation zone, in a range from 0 to 256. Arrows in chart point to the monthly NDVI pattern observed for the Meso-American corridor. The other lines correspond to the different areas in the southern distribution range.

Figure 4 shows the averaged monthly and yearly climate variables as recorded in the sites of tick collections. Both *B. annulatus* and *B. geigyi* are the species with preferences towards high temperatures. They have been mainly collected in areas were winter minimum temperature is above 15 °C. They prefer zones where maximum temperatures remain between 33 and 36 °C. The requirements for temperatures are always higher for *B. geigyi* than for *B. annulatus*. Both species have been collected in areas were maximum rainfall
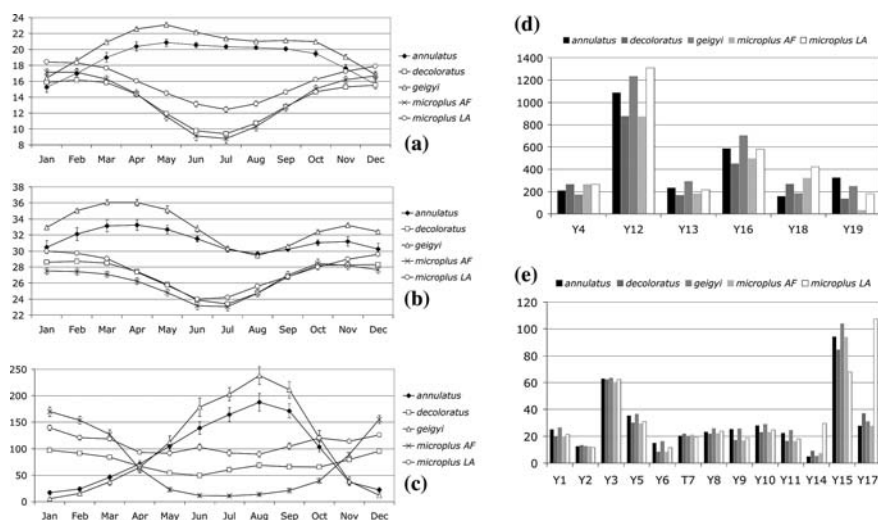
Figure 4. Mean monthly (a, b, c,) and yearly (d, e) values of climate variables recorded for the known collections of *B. annulatus*, *B. decoloratus*, *B. geigyi* and *B. microplus* (in both Latin America, LA, and Africa, AF). Figure 4a shows the mean minimum monthly temperatures recorded for collection points of the species, (b) the mean maximum temperatures, and (c) the mean monthly rainfall. Bars represent SD. Figures 4d and e display the yearly variables (Y) with a number according the list of variables in Material and Methods.

is recorded between June and September (Figure 4c). Populations of these two species support a period of low rainfall when temperatures are maximum. Both species have high requirements of annual precipitation, precipitation of wettest month and precipitation of wettest quarter (Y12, Y13 and Y16, respectively, higher for *geigyi*), while supporting the smallest values for the precipitation of the warmest quarter (Y18). It is interesting to compare the temperature preferences of both *decoloratus* and African *microplus*. While summer temperature requirements are higher for *microplus*, recorded values for winter are slightly lower than those observed for *decoloratus*. Minimum monthly temperatures are similar for *B. decoloratus* and the African populations of *B. microplus*, and both are around 4 °C less than the mean recorded for sites of collections of *B. microplus* in Latin America. The rainfall outline observed for *decoloratus* shows a pattern of low rainfall regimes, with minimum in May and June. The requirements of rainfall for *microplus* in Latin America are higher, while African *microplus* are concentrated in areas of very low rainfall between May and October, and high rainfall between November and March. The periods of high rainfall in African *microplus* coincides with the periods of maximum temperatures supported by these populations. Although African populations of *microplus* have requirements of high total rainfall, they can support long periods of dryness in winter. Figures 2d and e include the average values observed for the yearly variables. Critical differences can be observed in the precipitation of driest month, precipitation seasonality and precipitation of

driest quarter (Y14, Y15 and Y17) as related with American *microplus* records, for which precipitation seasonality is smaller than for other species and the total rainfall in the driest month and quarter is higher. Interestingly, preferences of American *microplus* for total precipitation show values three times higher than for other taxa analysed.

Figure 5 shows the cluster analysis as performed separately among the demes of each population. In this figure, each symbol corresponds to a record of the species, collected in one of the vegetation areas as separated by signature analysis of the NDVI monthly values. This kind of analysis provides information about the relative position within the space of ecological preferences, and the degree of ecological separation among the demes. The records of *B. annulatus* as well separated demes are easily appreciated, being the bottom-right records those collected around Mediterranean zones. However, sub-Sahelian records appear close to the rest of collections, meaning for similar preferences. Figure 5b displays the relative position of records of both *B. decoloratus* and African *B. microplus*, considered as a whole without separation in demes. It is easily observed that the preferences of *B. microplus* lie almost in the middle of the space of preferences of *B. decoloratus* ticks. Furthermore, it is observed (Figure 5c) that demes within *decoloratus* constitute a very heterogeneous assemblage. Critical demes lying in the border of the statistically homogeneous envelope of the species are those labelled as 25 (portions of Ethiopia, Democratic Republic of Congo and Cameroon, see also Figure 1) and 18 (much of the western distribution range, see Figure 1). Specimens within the deme labelled as 15 have been dispersedly collected in Eastern Africa, in small transitional areas of undifferentiated woodland, Zambezian miombo and zones of mosaic of evergreen bush land and secondary Acacia grassland. It seems that the main factor separating this deme from the main ecological preferences of the species is the relatively high altitude of collections, which causes lower temperatures. Collections for *B. geigyi* specimens show a clear separation among the only 4 demes analysed (Figure 5d). Demes 15 and 16 (collected in the sub-Sahara zones, with lowest NDVI values) are close one to each other in their climate preferences, while deme 20 (recorded in most vegetated parts of western Africa) has obvious differences with the formers. Specimens in deme 18 lie in an intermediate position between the remaining demes. The collections of Latin American *microplus* are very homogeneous according to their climate preferences (Figure 5e) and only deme 47 (present in the North-central moist Andes) appears as separated from the remaining tightly grouped demes.

Discussion

This study presents the distribution and climate preferences of four boophilid tick species in Africa and Latin America, from a database of tick collections including more than 24,000 edited records. Therefore, it is the most extensive
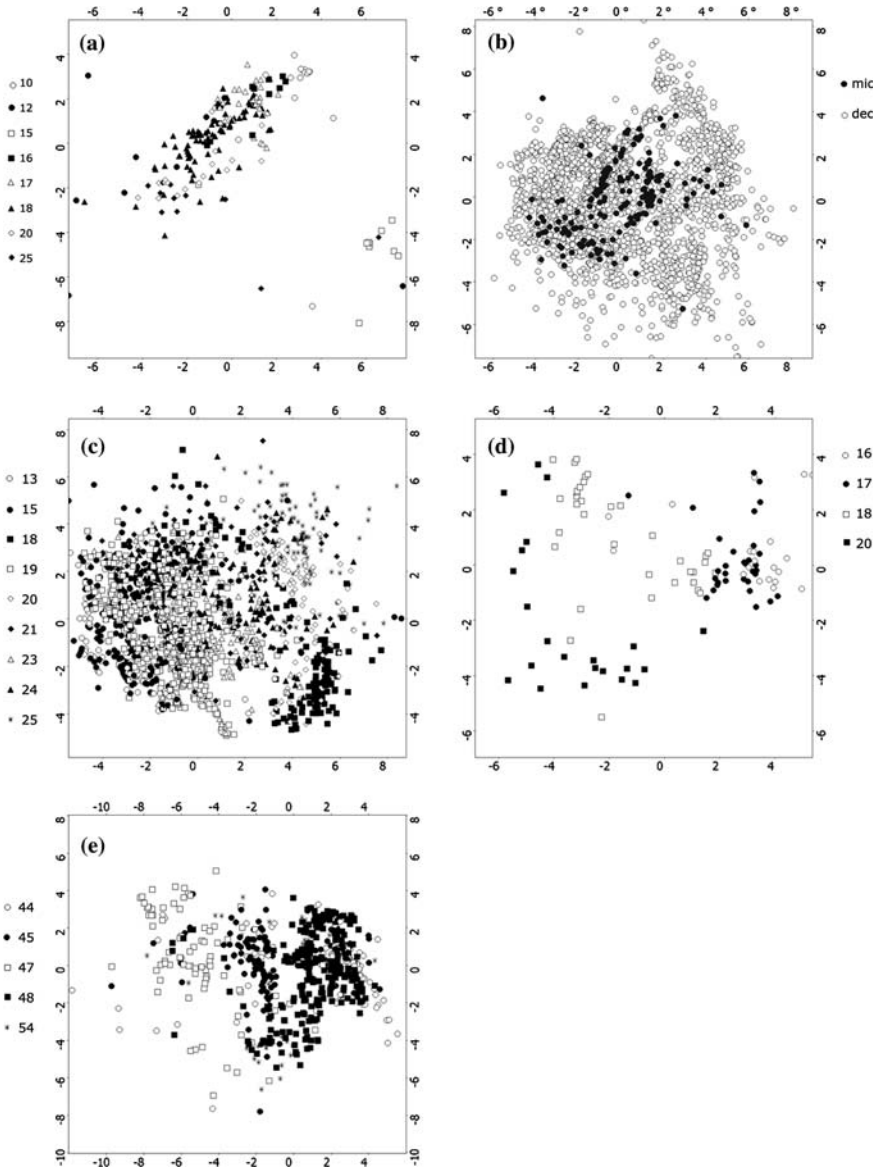
Figure 5. Cluster analysis of demes of *Boophilus* ticks, separated according to the classification of remotely sensed vegetation features (as displayed in Figures 1 to 3). Each symbol represents a deme, identified with a unique number, according to the vegetation category as displayed in previous figures. The charts show the coordinates in the factorial plane of the first two axes of the collections belonging to a given deme. (a) *B. annulatus*; (b) compared distribution of populations of African *B. microplus* (mic) and *B. decoloratus* (dec) without separation in demes; (c) *B. decoloratus*; (d) *B. geigyi*; (e) Latin American *B. microplus*. The analysis was not done separately for African records of *B. microplus* because the high dispersion of records.

and updated registry of the distribution of these ticks within the regions considered. Much work remains to be done with records of *B. microplus* in Asia and the distribution of *B. annulatus* in the former soviet republics. References for these regions lack adequate spatial references (Morel 1965), and accession to the original collections to check the species determination is sometimes difficult.

Cluster analysis has been used in this paper to compare the climate preferences of the involved species, by assessing the *n*-dimensional space of the climate variables as occupied by each species. Hutchinson (1957) defined the fundamental ecological niche as comprising those environmental conditions within which a species can survive and grow: a conceptual space whose axes include all the environmental variables affecting that species. Unsupervised classification of monthly composites of the Normalized Difference Vegetation Index (NDVI) has been explored to further divide each continent into areas with ecological meaning. The classification produces a set of categories based on the seasonal dynamics of NDVI, enclosing regions that are homogeneous within each category and statistically different between them, providing a framework to compare the ecological preferences of the tick populations of each species (called herein demes) collected in the regions. NDVI is an estimation of the vegetation stress and is not linearly correlated with single climate variables (Rasmussen 1998). This procedure together with cluster analysis on demes has been able to show the existence of significant differences in the climate data recorded for the demes within the same species. There is increasing evidence that the concept of undifferentiated species comprising individuals with broad tolerances is not correct (Davis and Shaw 2001). Intra-species variation makes it impossible to define precise limits to the climatic tolerance of a species since there is no guarantee that the limits for one deme at one range margin will be exactly the same as those for another deme at another margin. Predictive modelling of species geographic distributions based on the environmental conditions of sites of known occurrence constitutes an important technique in analytical biology. In this context, a niche-based model represents an approximation of a species ecological niche in the examined environmental dimensions. In a study over a large region, spatial variation exists in the environmental conditions available to the species. It is expected that, for large regions and with the usual spatial variations in environmental conditions, differentiated populations of the target species may exist, occupying different steps within the fundamental niche of the species. These populations are obscured when niche-based models are applied to the whole area of the species distribution. Given that the prediction engines are feed with every available record, geographically projected results can be dangerously biased if populations are not recognized and modelled separately (Osborne and Suárez-Seoane 2002).

Both *B. geigyi* and *B. annulatus* have been collected in areas displaying highest temperatures, and high seasonal rainfall. The known African distribution of the two species lies within a narrow band extending into the

parallels 10° and 20° N. *B. geigyi* is restricted to the warmer and more humid portions of western Africa, while *B. annulatus* extends further east. The later is also common in the Mediterranean basin. Both branches of the African *B. annulatus* distribution (Mediterranean and sub-Saharan) are clearly different according to cluster analysis, but these differences may be produced because the distinct seasonality in the climate recorded in both parts of the distribution range. Anyway, vegetation signatures are clearly different between these demes, those located in the Mediterranean and immediately south of Sahara having a low yearly NDVI, while those collected further south displaying high yearly NDVI values. Analysis of records of *B. geigyi* provides the separation into heterogeneous clusters, demes collected in central and south Mali clustering closely, and those recorded from the most western portions in Africa (around parallel 10° W) into a different group. It is of interest to note that the vegetation areas to which *geigyi* is associated extend further into east Africa. The absence of the species from eastern portions of the Continent may be due to misidentifications or to the absence of adequate prospective work in the zones. Both *annulatus* and *geigyi* may appear together as they share the main signature of NDVI in western Africa. Nothing is known about the compared seasonal activity of both species in the zones where their distribution overlaps.

Boophilus decoloratus is widespread in sub-Saharan Africa. It is absent from deserts and in the most humid parts of central Africa. It is a species with requirements of low temperature and rainfall, being present at most altitude ranges and almost under rainfall zones, being most common in zones obtaining 500–1000 mm per year, surviving in zones with an annual rainfall as low as 380 mm (Walker et al. 1978). *B. decoloratus* can survive in areas where there is a maximum of 90 days of frost spread over a period of 150 days a year (Gothe 1967). At lower temperatures there may be pockets of suitable climatic conditions where it can survive (Theiler 1949). Cluster analysis suggests a relative homogeneity within the demes collected through the continent. Only the specimens collected at the northern part of its distribution range (associated with areas of high and almost seasonally invariable NDVI) show a certain degree of heterogeneity when compared with other demes of the species. The remaining zonesto which it is associated show the same pattern in NDVI: a period of high NDVI values between January and July, then a sudden decrease of this index. In areas of western Africa, *decoloratus*, *annulatus* and *geigyi* may appear associated, but there is a trend for *B. decoloratus* to be located in areas of lower temperature and rainfall.

There is a clear contrast between climate preferences recorded for *B. microplus* in both Africa and America concerning monthly maximum temperatures (higher in American collections), precipitation of driest and coldest quarters (three times higher in American records) and rainfall seasonality (very marked in African collections). However, it must to be realized that high rainfall in the African records has been recorded in the summer period. Therefore, although total rainfall preferences are higher in *B. microplus* than in *B. decoloratus*, the former may stand in areas with relatively long periods of

dryness, probably synchronizing the cycle to avoid coincidence of critical phases with drought. Some references to the rainfall preferences of *B. microplus* in Africa points to high rainfall requirements, like the comments by Theiler (1962, "in all probabilities collected from well irrigated farms") Yeoman and Walker (1967, "must be considered a species of the high rainfall areas…from 400 to 1000 mm") and De Vos) 1979, "absent in areas where rainfall is less than 500 mm"). Seasonal rainfall changes supported by *B. microplus* have been reported as similar to those supported by *B. decoloratus* (Arthur and Londt 1973) as recorded in the current paper.

Cluster analysis between *B. decoloratus* and *B. microplus* shows that the African *B. microplus* are located within the *n*-dimensional ecological niche of demes of *B. decoloratus*. Therefore, the ecological preferences of African *microplus* cannot be extrapolated from those of American populations. In Africa, *B. microplus* had not invaded all areas that were climatically favourable for this species, as obtained by a modelling approach Sutherst and Maywald 1985). This failure was interpreted as being due to attempted interbreeding between *B. microplus* and *B. decoloratus*, resulting in a zone of sterile hybrids, which would present a barrier to further spread (Sutherst 1987). Several authors have discussed the mechanisms of the displacement of one species by the other. We think that previous models should be re-evaluated with the current knowledge of African *B. microplus* preferences. Anyway, there are large geographic areas at risk of colonization by *B. microplus* in Africa, if the tick should continue to spread from its present sites. The tick is common in parts of South Africa, Swaziland, Zimbabwe, where it was probably introduced from Mozambique in the mid-1970s (Norval et al. 1992) or Zambia, and already reported for other parts in Africa (Theiler 1962; McLeod and Mwanaumo 1978; Berkvens et al. 1998). The spread has been recently observed in Tanzania (Lynen, personal communication). Realistic simulations of the impact of climate on the spread of *B. microplus* in Africa will require a better understanding of the complex interactions between the many factors affecting distribution, including dynamic models to simulate the relationships between climate and the potential of the species to disperse through fragmented landscapes, and the relations between *B. microplus* and *B. decoloratus* on host.

The primary purpose of this study should then be regarded as an attempt to provide an accurate ecological basis in the building of predictive models of tick distribution under current and future climate conditions in the considered regions. Modelling strategies for predicting potential distributions of ticks have focused on the characterization of the bioclimate envelope (Cumming 2002; Olwoch et al. 2003; Estrada-Peña 2003). Some recent studies have questioned the validity of this approach by pointing to the many factors other than climate that play an important part in determining species distributions (Davies et al. 1998; Lawton, 2000). Concerning ticks, both dispersal ability by hosts and vegetation may have potential impact in the predictive mapping. However Pearson and Dawson (2003) concluded that the bioclimate envelope approach could provide a useful first approximation, stressing also the importance of the

spatial scale. The limit of the scale in our work and the accuracy of some records imposed a restriction to additional studies on associations with the vegetation. Cumming (2002) proposed that continental-scale distributions of ticks are principally determined by climate, and it is therefore suggested that many species distributions can in fact be considered to be in equilibrium with the current climate at the macro-scale. Genetic adaptation of species is rarely considered, being range shifts frequently seen as the expected response to the climate. It is usually expected that evolutionary change occurs only on long time scales and that the tolerance range of a species remains the same as it shifts its geographical range (Pearson and Dawson 2003). However, studies have shown that climate-induced range shifts can involve not only migration into newly suitable areas, but also selection against phenotypes that are poorly adapted to local conditions (Davis and Shaw 2001). The finding of *Boophilus* populations with statistically different climate preferences should be regarded as an additional problem in understand and map the climate factors responsible for tick distribution. Of particular importance is the divergence of African and American *B. microplus* populations and the apparent difficulty to capture the evolving ecological plasticity of tick populations.

Acknowledgements

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