Using ground-derived data to assess the environmental niche of the spinose ear tick, *Otobius megnini*

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Abstract

Four layers of environmental information, namely 1) monthly atmospheric temperature and rainfall, 2) annual ground and underground moisture, evaporation, surface adjacent specific humidity, and temperature, 3) monthly Normalized Derived Vegetation Index (NDVI), and 4) soil physical attributes, were used separately to define the expected geographical distribution and environmental niche of the spinose ear tick, *Otobius megnini* (Dugès) (Acari: Ixodida: Argasidae), an endophilic argasid, in both tropical and neotropical regions. The best predictive values were obtained from ground-derived climate. Air-derived features ranked second. The remaining environmental information had poor discriminatory abilities. The most informative variables in the distribution of neotropical populations are ground temperatures, with surface humidity ranking second. In the tropics, surface humidity is the most important factor delineating the distribution of *O. megnini*. Marginality scores are similar for tick populations in both biogeographical regions, but specialization factors are different, supporting the findings that both populations are regulated by different variables. Similarly, models trained with records of one biogeographical region and projected into the other one, resulted in poorer predictions than when trained with the homologous set of records. Populations of the tick in the tropics experience a different range of temperatures than their neotropical relatives, whereas marginality scores are similar. The conclusion is that each population uses particular portions of the environmental niche, probably because of different climate or competitor constraints on either biogeographical region.

Introduction

The spinose ear tick, *Otobius megnini* (Dugès) (Acari: Ixodida: Argasidae), is a one-host ectoparasite primarily of large wandering ungulates, and is thought to have had its original center of distribution in the arid lands of southwestern North America (Keirans & Pound, 2003). From that locality, it was introduced into Central and South America, Australia, and South Africa, whence it spread to Lesotho, Botswana, Namibia, Zimbabwe, Zambia, and Madagascar (Keirans & Pound, 2003; Mayberry, 2003). The larvae, as well as a variable number of nymphal stages, feed for long periods of time deep in the ear canal of their hosts. After the final nymphal stages have completed feeding, they drop from the host. The subsequent moult to adults, mating, oviposition, incubation of eggs, and larval eclosion and survival occur under the surface of the soil. *Otobius megnini* is of economic importance as a parasite of cattle, sheep, goats, and horses; furthermore, reports of human infestation are also quite frequent (Keirans & Pound, 2003).

Almost every species of soft tick (Acari: Ixodida: Argasidae) has developed a strategy towards so-called endophilic behaviour. They are 'burrow parasites', whose non-parasitic stages live in the nests of their hosts, and attach to the hosts when they are available. This strategy protects soft ticks from climatic extremes and permits them to colonize habitats in which external climatic conditions could be potentially detrimental to their survival. In contrast, exophilic ticks commonly restrict their distribution to narrow segments of a climate niche, lest their quest for hosts in an unprotected environment expose them to harmful external elements.

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Since the pioneering works on ticks (i.e., Hugh-Jones, 1989; Cumming, 2000), researchers have endeavoured to develop a methodology for mapping the potential distribution of some of the major tick species (i.e., Estrada-Peña & Venzal, 2006; Lynen et al., 2007), as well as to elucidate the probable impact of climate change and understand the principal factors regulating the spatial distribution of ticks (Cumming & Van Vuuren, 2006; Estrada-Peña & Venzal, 2007). These methods assume that each species occurs within specific ranges of environmental variables that are conducive to its survival and reproduction. Species occurrence can be predicted by the inclusion of appropriate variables into what are commonly referred to as climate suitability models: the relationships are generated from a sample of correlations of species' presence/absence with specific values for environmental variables. Although concerns have been raised about some assumptions made in the construction of these models (Thuiller et al., 2005), they remain an important tool in clarifying the relationships between living organisms and their environment.

The adaptation of soft ticks towards endophilic behaviour precludes a straightforward association between the presence of the ticks and a given set of climate or vegetation-derived features. This hampers the evaluation of the climate niche occupied by a species and the role of restrictive variables in delineating its distribution. Such sets of environmental features are commonly used for exophilic ticks in the demarcation of their habitat preferences. Climatic conditions that would otherwise potentially restrict the survival of a tick species would be cushioned by the protective effect of the ground layer, hence permitting the survival of viable populations. Endophilic traits thus require the determination of the usefulness of sets of data as markers for the suitability of habitats for soft ticks, different from those used for exophilic species.

The main purpose of this paper was to evaluate the performance of different sets of environmental data as markers of the recognized niche of the tick *O. megnini*. The second aim was to build models of distribution around the particular distribution of the tick on two sets of sites (tropics and neotropics). Furthermore, we used the recorded distributions of the tick in Africa and the Neotropics to ascertain by comparison of the most restrictive environmental variables, whether each population has evolved divergent preferences towards a given habitat niche.

Materials and methods

Sources of tick records

Records for *O. megnini* include the results of surveys performed in Argentina, South Africa, and Namibia during the last 20 years. Furthermore, published records for the neotropical region from Mexico to Argentina (compiled by SN and AAG) and for the tropics (originally compiled by Cumming, 2000) were used when accurate information on the locality of collection was available. The final set included 146 records of *O. megnini* in the neotropics and 405 in the tropics (Figure 1).

Environmental raster layers

Four sets of variables were used to outline the environmental niche. WorldClim is a set of interpolated climate values over the surface of the Earth (Hijmans et al., 2005). A complete explanation of interpolation procedures can be accessed at http://www.worldclim.org. This set is herein termed 'atmospheric climate', from which we used the monthly values of both minimum and maximum temperatures as well as rainfall at a resolution of 10°. We also used a series of monthly Normalized Derived Vegetation Index (NDVI) images captured at 0.1° resolution by NASA Earth Observations (NEO, http://neo.sci.gsfc.nasa.gov) between 2001 and 2007. The individual NDVI layers were processed to produce monthly averages at the nominal resolution across the above mentioned period. NDVI is a surrogate for photosynthetic activity, and it has been acknowledged as one of the best single variables in the recognition of habitat suitability for *Ixodes ricinus* (L.) ticks (Estrada-Peña, 1999). Environmental descriptive variables for both atmospheric climate and NDVI sets were used as monthly variables, instead of computing the mean and standard deviation of both temperature and rainfall.

Abiotic variables at ground level could potentially more adequately reflect the environmental niche of the targeted tick because of its endophilic behavior. We thus in addition used the GLDAS-DISC series of assimilation models including monthly values of evapotranspiration, humidity, and temperature at soil level, as well as temperature and moisture content at variable depths in the soil at a resolution of 0.25°. This set is herein called 'ground climate' and full details are available at http://agdisc.gsfc.nasa.gov/data/browse/GLDAS/GLDAS_NOAH025_M. This set has 11 monthly variables, leading to an unrealistically high number of colinearly correlated variables. It was therefore decided to work only with annual values. Monthly values were converted to mean, maximum, minimum, and standard deviation of evapotranspiration ($kg\, m^{-2}\, s^{-1}$), surface adjacent specific humidity ($kg\, kg^{-1}$), and temperature (°C) at ground level, as well as temperature (°C) and moisture ($kg\, m^{-2}$) content at depths between 1 and 10 cm below the soil surface. This procedure was designed to balance the inclusion of values involving one complete year and seasonality, whereas keeping to a minimum the number of variables that retain ecological significance. The fourth set

of environmental raster layers included soil physical characteristics (the ISRIC-WISE set; Batjes, 2005). This database included soil properties at a resolution of 0.5°. We utilized only the available quantitative variables, namely percentage of clay, sand and silt, total porosity (%), water retention capacity, conductivity, and terrain drainage. Qualitative variables for soil, according to the standard designations of FAO, were not included.

The resolution of the data layers used affects the results, as a specific grain size in descriptive variables must match the resolution of the database of tick records. A recent study by Guisan et al. (2007) compared the differences in model performance with a 10-fold change in grain size, as applied to 50 species, with 10 different model methodologies and applied to extents ranging from national to continental scales. Their results showed that difference in performance between fine- and coarse-grain models only reveal slight-to-moderate changes across techniques. Their conclusions were that change in grain size does not substantially affect species distribution models. On the other hand, improvements of the model fitting could be expected with an adequate combination of explanatory variables from separate datasets. However, because of the different resolutions, this could be performed only after downscaling or upscaling some variables, which are difficult to interpolate (i.e., soil attributes). Consequently, each set of originally obtained environmental variables was used separately.

Fitting niche-based distribution models

There is considerable controversy about how to best measure performance of the models, and the influence of autocorrelation on such a measurement. One example is the problem of non-independence between data used for calibration of models and that used for validation (Araújo et al., 2005). Non-independence is often the result of using spatially autocorrelated data to calibrate and validate the models, and one of the consequences is that the perceived ability of models to make realistic predictions may be inflated (Segurado et al., 2006). If the values of a variable depend on the distance between sample points, a set of closely spaced observations effectively provides less information than the same number of observations more widely separated in space. This could be a serious shortcoming in models, as species' occurrences tend to be aggregated at most spatial scales, and the more aggregated species' occurrences are, the more likely it is that environmental variables will show some explanatory power simply because of the fact that environmental conditions tend to be more similar at neighbouring sites (Segurado et al., 2006). Patterns of species' distributions may be spatially autocorrelated because of contagious population dynam-

ics and historical factors, but they may also be the result of spatial structure among environmental predictors (Storch et al., 2003). Species and the environment may share spatial structure because of the effect of spatially structured environmental predictors and non-environmental contingencies that may or may not be related amongst them (Borcard et al., 1992). Segurado et al. (2006) studied the effect on final performance of models of two methods to account with spatial autocorrelation and concluded that forcing the inclusion of a covariate term to cancel spatial autocorrelation of species distribution represents a problem, first because models tend to underestimate the importance of environmental variables that co-vary with species' occurrences, second because those models cannot be extrapolated to regions where no occurrence data are available. Therefore, we decided not to include a covariate term in our modelling methods.

The reliability of different modelling algorithms to project the niche preferences of an organism is also subject to debate (Elith et al., 2006). Different modelling techniques calibrated on the same species can produce different results. A preliminary test (results not included) using presence + absence algorithms based on two sets of sites (tropics and neotropics) in which the tick was absent after active surveillance provided considerable bias in the output of the different algorithms, ascribable only to the use of different absence or pseudo-absence layers. We then used a method based on presence-only data, the MaxEnt algorithm version 3.2.1, originally developed by Phillips et al. (2006). This algorithm produces predictions from incomplete information by estimating the most uniform distribution of points of occurrence across the area of study. This maximum entropy method has emerged as one of the three most reliable techniques for predicting species distributions (Elith et al., 2006). The method outputs an estimated probability of occurrence of the tick for every cell of the grid, using a set of pseudo-absence data as background information.

Models were trained separately for the tick records in the tropics and the neotropics, as one of the aims of the current study was to test whether different restrictive variables are applicable to each population in its particular environmental niche. Testing or validation is required to assess the predictive performance of the model. The most commonly used approach is to partition the data randomly into 'training' and 'test' sets, thus creating quasi-independent data for model testing (Fielding & Bell, 1997; Guisan et al., 2007). Model validation statistics were based on 10 replicate random partitions of the localities into the test (25%) and training (75%) data. For each replicate, we calculated the number of test localities omitted from the prediction and applied a binomial test to check

statistical significance. The validation test required the use of a threshold to define 'suitable' and 'unsuitable' areas, so we adhered to the approach of Pearson et al. (2007) by using the lowest presence threshold (LPT). LPT is a relatively conservative index because it identifies sites that are at least as suitable as the lowest value associated with the presence of the species. The more customary receiver operating characteristic analysis was not used because of recent criticism about bias (Lobo et al., 2007). Explanatory variables are defined as most informative when they have the greatest influence on the final model. These variables are considered to be the most suitable for the description of an organism's environmental niche. To determine such a set of variables, the increase in regularized gain is added to the contribution of the corresponding variable in each iteration of the training algorithm, or subtracted from it if the change to the absolute value of lambda is negative.

We were interested in assessing whether tropical and neotropical populations of the tick use different portions of the available environment, either because of diverging evolution towards different niches or because of different constraints within their actual niches in the two regions of distribution. Niche overlap among the tropical and neotropical populations was checked using the methods reported by Peterson & Holt (2003). The best model was used to predict the geographical distribution of each population (autopredictions) and those of the other population (allopredictions). We used the ratio of alloprediction to autoprediction as an inverse measure of inter-population niche differentiation or niche overlap; the greater this value, the less the apparent difference of geographical variation in a species niche (Peterson & Holt, 2003). We further used herein the approach developed by Hirzel et al. (2002) to check the relationships of the recorded tick distribution and their corresponding available niche in both tropics and neotropics. The method computes a group of uncorrelated factors from the raw environmental information that provided the best model, summarizing the main environmental gradients in the region considered, similarly to common ordination techniques such as Principal Component Analysis. However, it derives these factors using data only from known species presence, thus providing factors with biological meaning. The first axis (marginality factor) is chosen to describe the marginality of the niche with respect to the regional environmental conditions, by maximizing the difference between the environmental mean value of the species' presence, and the global mean environmental value of the entire region studied. The following axes (specialization factors), sorted according to decreasing amounts of explained variance, were used to represent the species' degree of specialization in the rest of the (orthogonal) environmental gradients identified in the study area. Biomapper 3.1 software
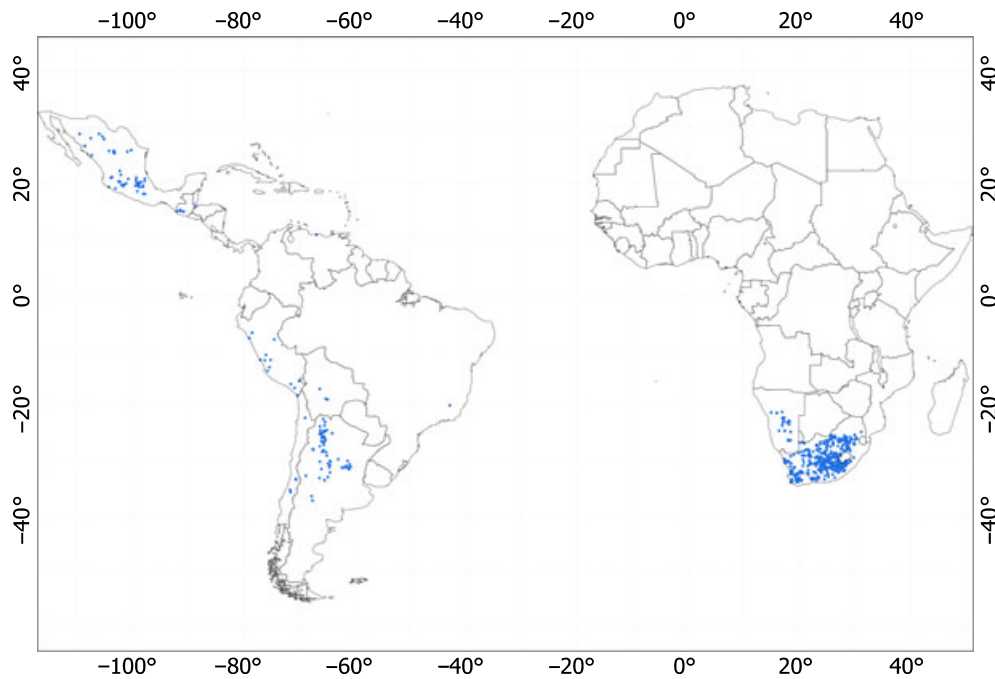
Figure 1 Map of the tropical and neotropical regions displaying the locality records used in determining the distribution of *Otobius megnini*. Dots represent the reported presence of the tick.

(Hirzel et al., 2002, see http://www.unil.ch/biomapper) was used to calculate marginality and especialization.

Results

For predictions applied to tropical (T) and neotropical (N) populations, the LPT scores were 0.12 and 0.11, respectively, with a mean omission error of 0.02 and 0.06, respectively, and 9/10 partitions recording minimum training presence at a binomial probability of P<0.05 using the GLDAS-DISC data set of ground climate. For the atmospheric climate set, the LPT values were 0.10 and 0.12, respectively. Omission error for T occurred in 2/10 replicates and P = 0.11; omission error for N occurred in 1/10 replicates with P = 0.12. NDVI series provided LPT values of 0.07 and 0.11 for T and N, as well as higher omission errors (P = 0.29 and 0.25, in 5/10 and 4/10 replicates, respectively, for T and N). Errors were higher when

ground-derived physical attributes were used (P = 0.41 and 0.39, in 6/10 and 6/10 replicates, respectively, for T and N, with LPT values of 0.31 and 0.22). Therefore, the ground-derived climate value is the better descriptor for the niche of *O. megnini*. This best model captured 403/405 and 142/146 tick records in T and N. Figures 2 and 3 show the geographical range of suitable niches for T and N, respectively, computed using the different sets of descriptive variables.

Most informative variables in the delineation of climate niches for *O. megnini* are those which resulted in the maximum gain of the model when used in isolation (i.e., the most useful information by itself). Regarding neotropical populations and the ground climate set, most informative variables were the annual mean, maximum, and minimum temperature at ground level and depths of 1–10 cm. Mean and minimum humidity at the same depths were of secondary significance. Standard deviations of both annual
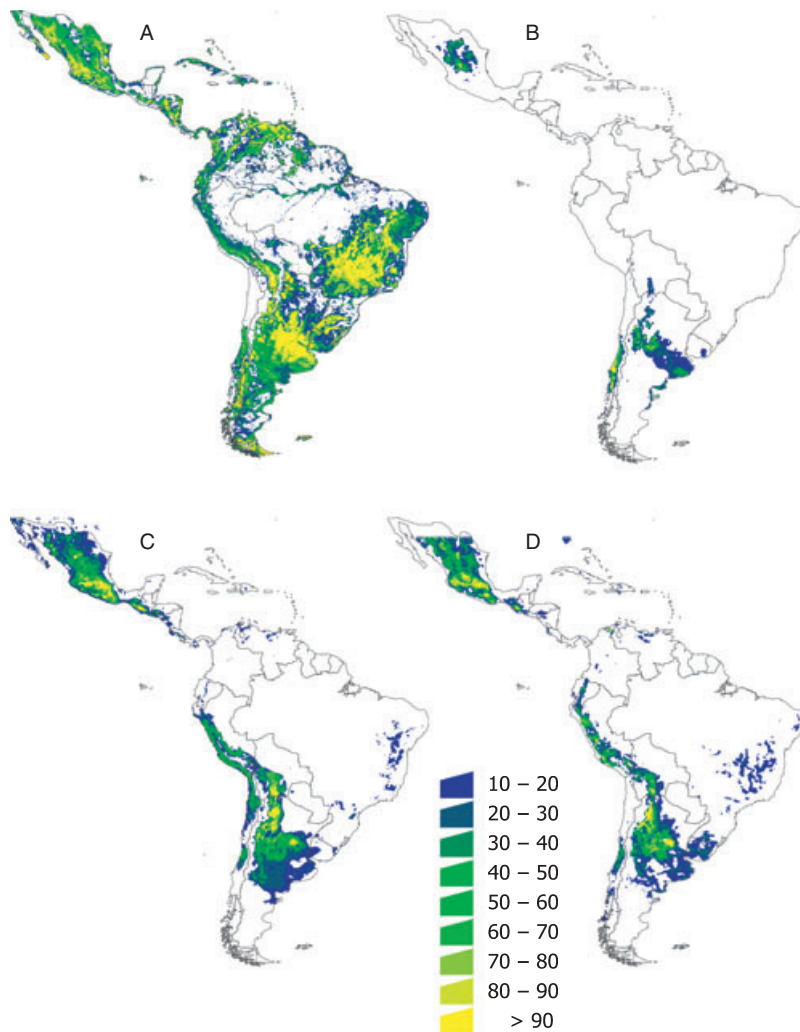
Figure 2 Extent of environments suitable for *Otobius megnini* in the neotropics using four sets of environmental information. Minimum suitability is displayed in blue, and maximum in yellow. Data layers used to develop each model were: (A) monthly Normalized Derived Vegetation Index (NDVI) values for the period 2001–2007, (B) physical characteristics of the soil, (C) monthly air climate values including rainfall and minimum and maximum temperature (1970–2000), and (D) annual values recorded between 2000 and 2007 for temperature, evaporation, and moisture at ground level, and temperature and moisture content at depths of 1–10 cm below ground surface.
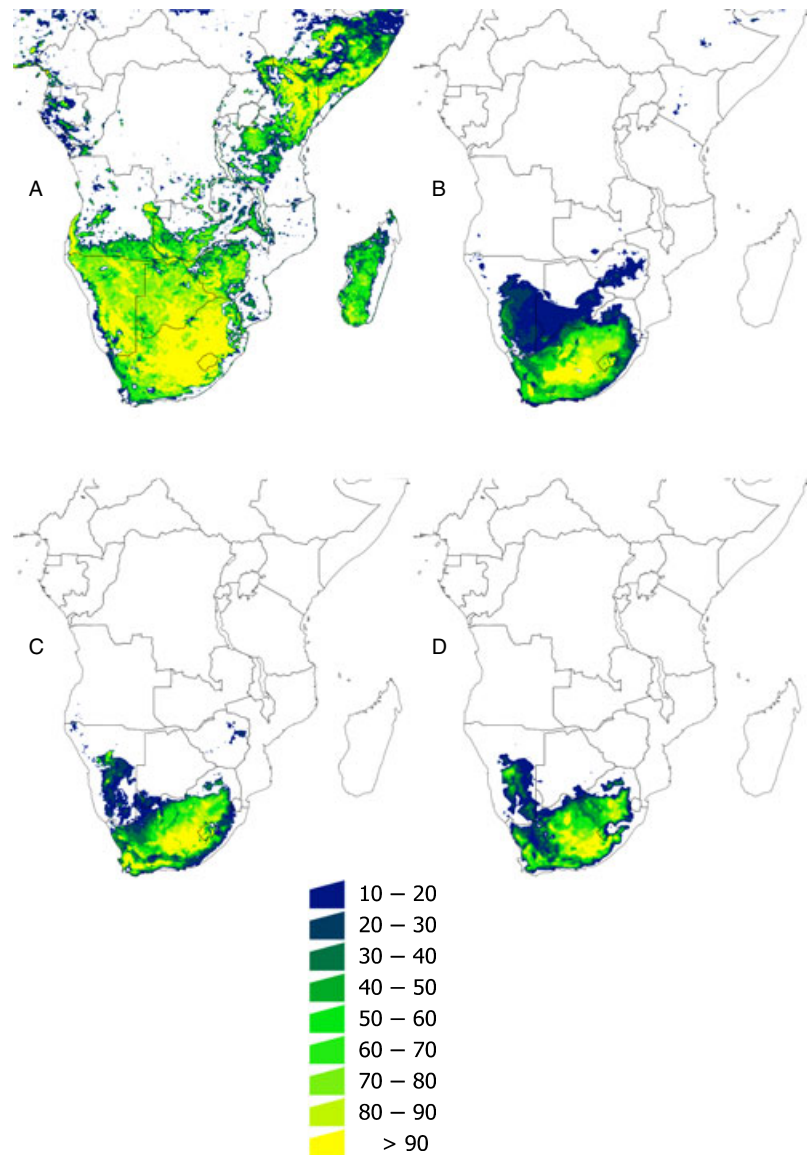
Figure 3 Extent of suitable environment for *Otobius megnini* in the tropics using four sets of environmental information. Minimum suitability is displayed in blue, and maximum in yellow. Data layers used to develop each model were: (A) monthly NDV1 values for the period 2001–2007; (B) physical characteristics of the soil; (C) monthly air climate values including rainfall and minimum and maximum temperature (1997–2000); and (D) annual values recorded between 2000 and 2007 for temperature, evaporation, and moisture at ground level and temperature and moisture content at depths of 1–10 cm below ground surface.

temperature and humidity, as well as all variables derived from evaporation, were not significant. Amongst the atmospheric climate set, temperature and rainfall between November and April (summer in the region) resulted in the highest gains in the model. The most informative NDVI variables for neotropical populations were the values between November and May. Every variable derived from the physical attributes of the soil was selected as being of high-ranking importance in the final model, even if that model provided a poor fit with actual records. Regarding tropical populations and the ground climate set, most informative variables were maximum and minimum moisture, with mean, minimum, and standard variation of temperature rated second. Models built with the atmo-

spheric data set pointed to precipitation from April to September as the most informative variables, whereas temperature during the same period was ranked second. Values between May and September were the better explanatory NDVI variables for the niche of *O. megnini* in the tropics. As with the neotropical populations, the models indicated that all soil attributes were of high significance.

Marginality and specialization were computed only for the set of ground-derived climate. The first selected axis, which maximizes the absolute difference between global environmental mean and the species mean (the marginality factor), explained 64% of the specialization for neotropical populations and 62% for tropical ones. These high

Table 1 Marginality and specialization scores obtained from the analysis of ground-derived climate values for the delineation of climate niche of *Otobius megnini* using the training set. The final set of variables included mean, maximum, minimum, and standard deviation of evapotranspiration (kg m⁻² s⁻¹), surface adjacent specific humidity (kg kg⁻¹) and temperature (°C) at ground level, as well as temperature (°C) and moisture (kg m⁻²) content at depths between 1 and 10 cm below the soil surface

Neotropical populations			
Marginality factor	64%	Specialization factor	21%
Mean temperature (ground)	0.80	Mean humidity (ground)	0.82
Minimum temperature (ground)	0.64	Minimum humidity (ground)	0.32
Mean temperature (1–10 cm depth)	0.11	Minimum temperature (ground)	0.11
Mean humidity (ground)	−0.12	Maximum temperature (ground)	−0.12
Tropical populations			
Marginality factor	62%	Specialization factor	19%
Mean humidity (ground)	0.83	Mean temperature (ground)	0.79
Mean humidity (1–10 cm depth)	0.41	Mean temperature (1–10 cm depth)	0.65
Maximum temperature (ground)	0.18	Minimum temperature (ground)	0.05
Mean temperature (1–10 cm depth)	0.01	Maximum temperature (1–10 cm depth)	−0.02

percentages of specialization pointed out the importance of these first factors in explaining both marginality and niche breadth of each of the two populations. Mean and minimum temperatures were the variables with higher marginality coefficients for neotropical populations, showing that the scores of these variables in the presence cells differed from the mean values in the region (Table 1). Mean humidity at ground level had a higher coefficient of the specialization factor. Mean and minimum temperatures were the variables related to the marginality factor of tropical populations (Table 1). It is important to notice that both populations had a similar marginality, whereas the variables associated with marginality and specialization factors were different.

Figure 4 represents a comparative overview of temperature and humidity at ground level recorded for the environment and for the tick presence sites in the tropics and the neotropics. These variables were chosen because they are the most informative for niche delineation as well as marginality and specialization factors. Tropical populations of *O. megnini* were absent from sites with temperatures higher than 15 °C because these sites had low humidity values. However, sites within the range of temperatures higher than 15 °C in the neotropics were always within a range of humidity higher than 0.008 kg of water. Autoprediction was 99.5% for neotropics and 97.2% for tropics. However, alloprediction varied greatly between populations. Models trained for the neotropical records produced a 97% of alloprediction when projected into the tropics, at the cost of 32% false-positive cells (Figure 5). Models trained with the tropical records showed 52% alloprediction when projected onto the neotropics, with 35% false-negative cells. In summary, marginality scores supported the hypothesis that both populations occupy a similar fraction of the available niche. Values obtained for alloprediction and the different involvement of variables in the specialization factors pointed to the hypothesis that both populations occupy a different portion of the available niche in either tropics or neotropics.

Discussion

This study reports the first assessment of the niche occupied by a soft tick that spends its non-parasitic stages under the surface of the soil, or in cracks and crevices in poorly maintained premises (Dreyer et al., 1998). The cushioning effect of refuges associated with that endophilic life strategy is likely to enable *O. megnini* to expand its distribution into areas otherwise unsuitable for its survival. Therefore, the tick depends heavily upon an adequate niche for the non-parasitic stages to complete their life cycle. Considering that poorly maintained premises constitute a suitable
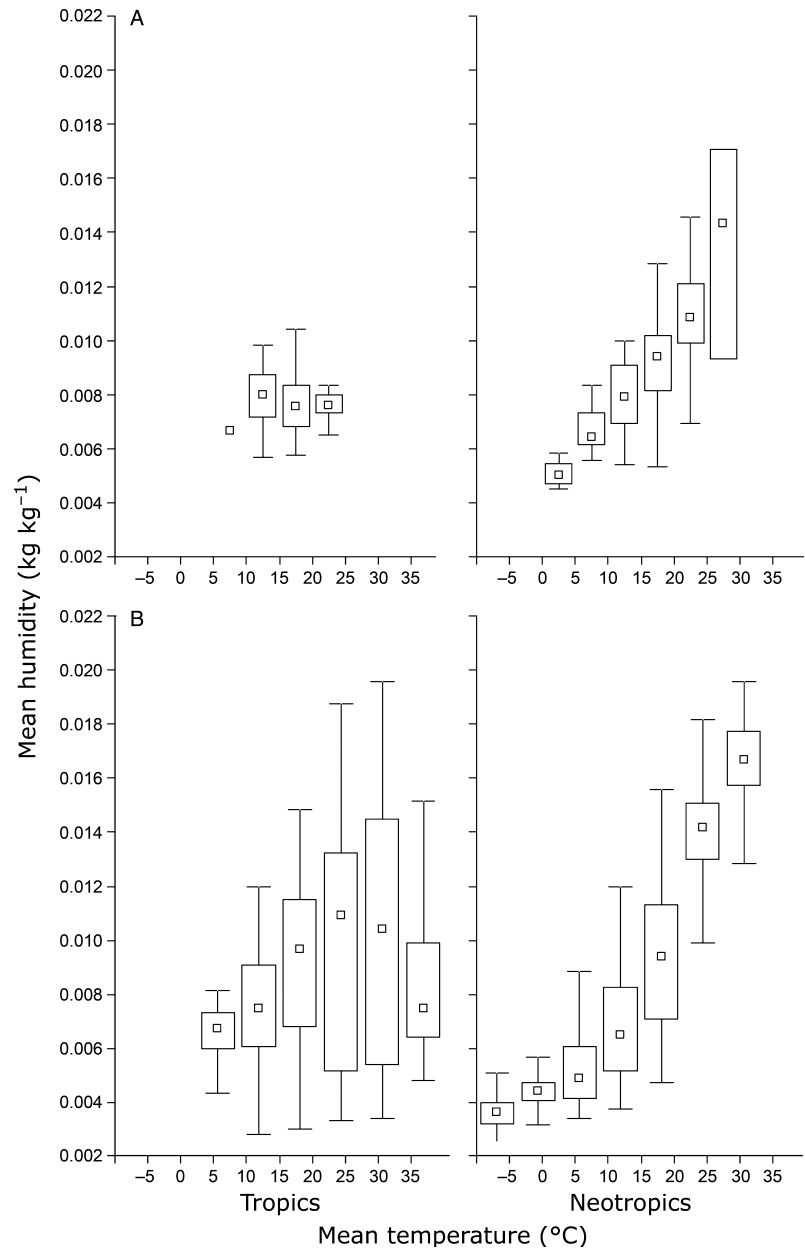
Figure 4 Average range of climate conditions recorded for sites where *Otobius megnini* was present in the tropics and neotropics, compared with background values (pseudo-absence set of MaxEnt algorithm). Temperature at the ground surface (in °C) and humidity at the same level (in kg of water per kg of soil) were selected to illustrate differences. (A) Sites where *O. megnini* has been recorded and (B) pseudo-absence set.

environment for the non-parasitic stages, it is important to also consider the human influence in the establishment of *O. megnini*. This influence is, however, probably more significant for the local spread of the tick than in the determination of its distribution at a regional level.

Because of the inherent difficulty of interpolating data sets into a common scale without introducing important errors, we purposely adhered to two recent findings in the field. First, that changes in the grain scale of explanatory variables have little effect on final model results (Guisan et al., 2007), and second, that there is no way to handle the

spatial autocorrelation without introducing covariate terms in models (Segurado et al., 2006). Choosing a grain size for modelling is partly a technical issue. For instance, grain size is related to the grid cell size of available environmental data or characteristics of the species data [e.g., geographical accuracy, sample size, or field survey constraints (Huettmann & Diamond, 2006)]. Changing the grain size can influence the perception of a phenomenon, such as patterns of presence. However, the above-mentioned study showed that there are no reasons to consider that grain size will always inflate a given modelling procedure. In any
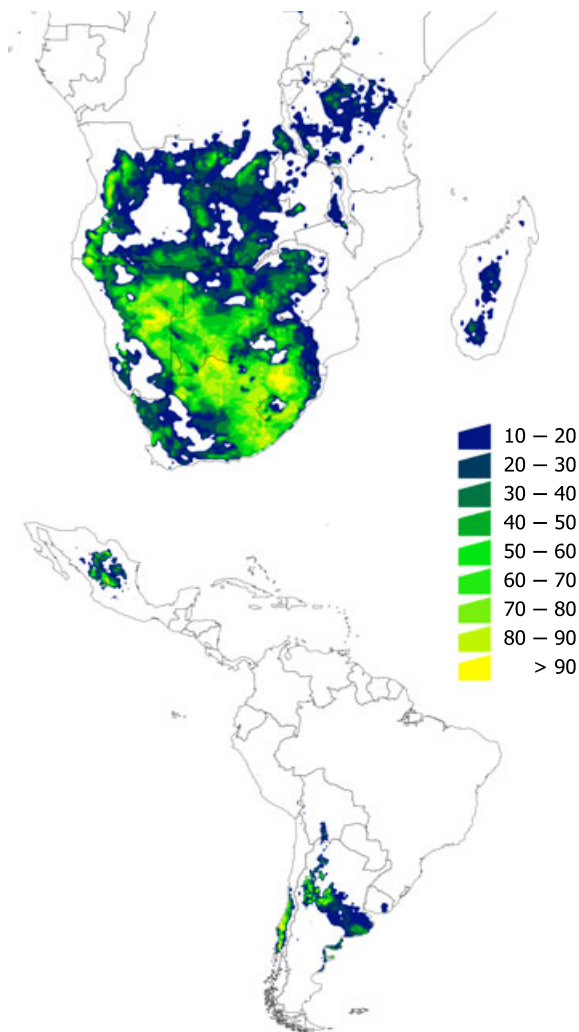
Figure 5 Projection of the predicted habitat suitability for populations of *Otobius megnini* in the tropics and the neotropics using models trained with records of the alternative region. Models were trained with records of each region using the set of ground climate values, and then projected onto the other region.

case, the resolution of the records database was higher than the resolution of the explanatory variables. In measurement of model performance, an overestimation of the model may occur both because of spatial autocorrelation between the calibration and validation data sets and spatial autocorrelation within explanatory variables (Segurado et al., 2006). When there is more than one candidate variable to explain a species' distribution, the assessment of the effect of spatial autocorrelation on models requires a more complex and thorough approach. Nevertheless, even if spatial autocorrelation inflates variable significance, this

does not mean that the final model configuration will exclusively include the most autocorrelated variables. The thorough study by Segurado et al. (2006) concluded that the inclusion of a contagion term to cancel spatial autocorrelation tended to underestimate the importance of environmental variables that co-vary with species' occurrences. We adhered to that conclusion and decided not to force the inclusion of such a contagion term.

The two climate data sets (atmospheric and ground-derived) performed almost equally well in the description of the tick niche. Best predictive ability was obtained with a set of climate variables obtained above and below ground surface, including temperature, humidity, and evaporation at a temporal resolution of 1 year. Entering monthly (atmospheric) variables may not be a suitable alternative for the detection of *O. megnini* niche, as the seasonal pattern of activity of the tick may vary even within a locality (Theiler & Salisbury, 1958; Drummond, 1967; Gugliel-mone & Mangold, 1986). As stated by Nava et al. (2009), photoperiod does not drive the seasonal regulation of *O. megnini*, and the factors governing dissimilar seasonal patterns remain largely unexplored. We did some tests based on the atmospheric data set included as yearly means and standard deviations of every variable, which provided poorer results (data not included) probably because of the low number of explanatory variables.

The use of remote sensing in modelling is based on the capture of measurements of radiation from a satellite and their links to the species to be mapped (Crombie et al., 1999). The NDVI is the most commonly used vegetation index in vector-borne disease-related studies (Kitron & Kazmierczak, 1997). This index has been used to classify habitat suitability for various arthropods, such as the ticks *Ixodes scapularis* Say (Ogden et al., 2006) and *Ixodes pacificus* Cooley & Kohls (Eisen et al., 2006), *Anopheles* spp. mosquitoes (Shililu et al., 2003), and *Culicoides* spp. (Purse et al., 2004). Its usefulness, however, seems to be poor when applied to *O. megnini*. This can most probably be ascribed to the lack of correlation between the preferred sites for tick development and the seasonal dynamics of the surrounding vegetation, as already mentioned for other tick species by Cumming (2000). Poor results were also obtained when the physical attributes of the soil were used. Soil characteristics do not satisfactorily represent the limiting variables for an endophilous tick, as they do not include essential variables such as the effect of temperature on development or the effects of rainfall on survival.

The differences identified in models trained with records from the tropics or the neotropics and further projected onto the other region are striking. These differences are further confirmed by the results of marginality and specialization scores, and the comparison of critical

variables between environment and sites of reported tick presence. Although the overall significance of these results is difficult to ascertain, they might provide evidence of different mechanisms of adaptation among tick populations. The invasive range of a living organism is hard to determine based only on its recorded occurrence, because it is subject to various environmental pressures, including climate and competitors (Thuiller et al., 2005). Environmental constraints within the new (invaded) habitat may have exerted different levels of pressure, directing evolution of the imported population. Furthermore, the geographic origin of the founder propagules and the representativeness of the genetic pool of the total population could have major implications for their ability to spread into new areas. The present study indicates that tropical populations of *O. megnini* colonize only a small fraction of the habitat that should be suitable according to the preferences of neotropical populations. Analysis of ground climate recorded at the capture sites of both populations indicates differences in restricting variables. Whereas temperature is a limiting factor for the tick in the neotropics, humidity is the main limiting factor for tropical populations, with temperature playing only a secondary factor. An analysis of the distribution of temperature and humidity values in both tropics and neotropics clearly indicates that sites with temperature higher than 15 °C over the ground surface are associated with low values of soil humidity in the tropics, whereas these sites are associated with higher ground humidity values in the neotropics. Our interpretation is that distribution in the tropics is primarily delineated by the ground humidity, preventing the tick from colonizing sites within the preferred range of temperature values. Because models trained for neotropical records consider moisture as a variable of secondary interest, the model projected onto the tropical region overestimates the suitable area and overpredicts the distribution of *O. megnini*.

Further studies on the predictive value of environmental information derived from the nearctic range of distribution of the species, from where it is argued that the tick originated (Keirans & Pound, 2003), together with empirical data on the factors regulating seasonal activity, and phylogenetic comparisons between populations, should provide a greater understanding of the regulatory and invasive processes accompanying the spread of *O. megnini*.

Acknowledgments

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