CHAPTER 2

Simulating tick distributions over sub-Saharan Africa: the use of observed and simulated climate surfaces

Simulating ticks distributions over sub-Saharan Africa: the use of observed and simulated climate surfaces.

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ABSTRACT

Aim

A broad suit of climate datasets is becoming available for use in predictive species modelling. We compare the efficacy of using interpolated climate surfaces (CRES and CRU) or high-resolution model derived climate data (DARLAM) for predictive species modelling, using tick distributions from sub-Saharan Africa.

Location

The analysis is restricted to sub-Saharan Africa. The study area was sub-divided into 3000 grids cells with a resolution of 60 x 60 km.

Methods

Species distributions were predicted using an established multivariate climate envelope modelling approach and three very different climate datasets. The recorded variance in predicted species distributions across the climate datasets was quantified by employing omni directional variograms. To further compare the interpolated tick distributions that flowed from using three climate data sets, we calculated true positive (TP) predictions, false negative (FN) predictions as well as the proportional overlaps between observed and modelled tick distributions. In addition, the effect of tick dataset size on the performance of the climate datasets was evaluated by performing random draws of known tick distribution records without replacement.

Results

The predicted distributions were consistently wider ranging than the known records when using any of the three climate datasets. However, the proportional overlap between predicted and known distributions varied as follows: for *Rhipicephalus appendiculatus* Neumann (Acari: Ixodidae), these were 60%, 60% and 70%; for *Rhipicephalus longus* Neumann (Acari: Ixodidae) 60%, 57% and 75%; for *Rhipicephalus zambeziensis* Walker, Norval & Corwin (Acari: Ixodidae) 57%, 51%, and 62%, and for *Rhipicephalus* capensis Koch (Acari: Ixodidae) 70%, 60%, and 60% using the CRES, CRU and DARLAM

climate datasets respectively. All datasets were sensitive to data size but DARLAM performed better when using smaller species datasets. At a 20% data sub-sample level, DARLAM was able to capture more than 50% of the known records and captured more than 60% of known records at higher sub-sample levels.

Main conclusions

The use of data derived from high-resolution nested climate models (e.g. DARLAM) provided equal or even better species distribution-modelling performance. As the model is dynamic and process based, the output data are available at the modelled resolution, and are not hamstrung by the sampling intensity of observed climate datasets (~ 1 sample / 30 000 km^2 for Africa). In addition, when exploring the biodiversity consequences of climate change, these modelled outputs form a more useful basis for comparison with modelled future climate scenarios.

INTRODUCTION

Predictive species modelling is rapidly becoming a routine analytical procedure (for review see Guisan & Zimmermann 2000), and with rapid advances in climate data interpolation and modelling techniques, it is now possible to predict the distributions of an array of insects, pests and pathogens using their major climate drivers (Messenger, 1959; Sutherst & Maywald, 1985; Meats, 1989; Perry *et al.*, 1990; Randolph & Rogers, 1997; Sutherst *et al.,* 1995; Coakley *et al.,* 1999; Cumming, 2000a; Rogers & Randolph, 2000; Randolph, 2001, 2002; Erasmus *et al.,* 2000, 2002; Harvell *et al.*, 2002). Many of these approaches are static and probabilistic in nature but remain the primary approach available for studying the possible consequences of changing environments on species distributions.

The principal sources of climate data used for predictive distribution modelling are climate surfaces, generated by interpolating observed climate data that was sampled at varying intensities from across a region. Consequently, any differences between these climate surfaces can usually be attributed to the spatial and temporal evenness of the observed data used for interpolation. Most modern interpolation techniques are pattern based and statistically incorporate horizontal as well as vertical (altitudinal) adjustments (see Hutchinson, 1989, 1991; Hutchinson & Gessler, 1994).

General circulation models (GCMs) have now become the primary method of simulating climates. These are coupled ocean-atmosphere models that provide 3-dimensional simulations of the atmosphere. To date, general circulation models (GCMs) have produced climate data at a horizontal resolution that is too coarse for use in predictive species modelling (> 100 km 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 prevent GCMs from being run at mesoscale grid resolutions (10 - 100 km). A potential alternative source of high-resolution climate data for use in predictive species modelling is nested limited-area models. Nested climate modelling 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. This technique provides a viable alternative to the use of observed/interpolated climate surfaces for fine scale climatic data. The resolution attained by this dynamic modelling process is essentially limited by the computing power available to the modellers.

The present study used one species distribution modelling procedure (Erasmus *et al.*, 2000) and three climate datasets (2 interpolated and 1 modeled) to evaluate the relative performance of the climate datasets in simulating the present distributions of ticks in sub-Saharan Africa. We employed distribution data from 4 tick species from the genus *Rhipicephalus.* These tick species are taxonomically well known, are poorly sampled and their environmental dependencies not adequately documented (Tukahirwa, 1976; Rechav, 1981; Short & Norval, 1981; Norval *et al.*, 1982; Horak *et al.*, 1983, 1995; Perry *et al.*, 1990; Rogers & Randolph, 1993; Cumming, 1998, 1999a, Walker *et al.*, 2000). As principal vectors of numerous cattle diseases these tick species are also of significant economic importance to the continent.

MATERIALS AND METHODS

CRES climate data

The first climate dataset used forms part of a topographic and climate database for Africa developed by the Center for Resource and Environmental Studies (CRES)(Hutchinson *et al.,* 1996) at the Australian National University. These data contain grid box values of elevation (Hutchinson, 1989), monthly mean climate of rainfall as well as daily values for maximum and minimum temperatures at a spatial resolution of 0.05 x 0.05 degrees. Climate grid box values were calculated by fitting topographically dependent climate surfaces to point climate data using procedures described in Hutchinson (1991) and Hutchinson & Gessler (1994), thereafter the surfaces were interrogated using elevations from the topographic data (McMahon *et al.*, 1995). Climate data at a sufficient spatial density to support reliable spatial interpolation were compiled. In addition to data already obtained by CRES, monthly climate data were acquired from many other research agencies. Data were collected over all available years to maximize spatial coverage, subject to the condition that rainfall averages were calculated from records of at least five years. The data set comprises data collected between 1920 and 1980 from approximately 1 500 temperature and 6 000 rainfall stations. The error of grid values depends mainly on the accuracy of the underlying climate surfaces. The standard errors of the temperatures are about 0.5 °C, while standard errors for rainfall range between 5% and 15 % (depending on data density and the spatial variability of observed mean monthly rainfall values). The mean monthly rainfall values as well as maximum temperatures for January and July are depicted in Figure 1. The climate surfaces are relatively smooth due to their dependency on low-resolution point observations. These data were re-sampled to the finest common resolution between climate data sets, which is the 60km x 60km DARLAM grid cells. This resulted in data for 3000 grid cells which was within the limitations imposed by the available hardware and software. The mean values of CRES data cells contained within each 60km x 60km grid cells was used as the new re-sampled CRES data value for that particular grid cell. Although some variation was lost in this procedure, between-cell variation before re-sampling was small due to interpolation between remote data points, and therefore the predictive ability of this data was not affected. After re-sampling, 92% of the grid cells had standard deviations smaller than 5% of the mean value for that particular grid cell. The variograms of re-sampled data in Fig 2 confirms this fact, with neighbouring cells remaining highly autocorrelated at small distances (~60km). We regard this small change in variation as reasonable for our purposes.

CRU climate data

The 1961 - 1990 climate dataset from the Climate Research Unit (CRU) was used as a second dataset (New *et al.*, 1999). The database consists of mean monthly climate fields with a 0.5° x 0.5° grid resolution across the global terrestrial areas, excluding Antarctica.

The mean climate surfaces were constructed from a 30-year (1961-1990) station observation field. The station data were interpolated as a function of latitude, longitude and elevation using thin-plate splines. The accuracy of the interpolations are assessed using cross-validation and by comparison with other climate surfaces (New *et al.,* 1999). Considerable spatial and temporal variance of climate surface variables over southern Africa can be observed in the CRU data (Engelbrecht *et al.,* 2002). Despite this, the climate surfaces remain smooth due to their dependence on low-resolution point data. The mean monthly rainfall values as well as maximum and minimum temperatures are depicted in Figure 1. These data were also re-sampled to 60km x 60km grid cells in the same manner as the CRES data.

DARLAM climate data

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

In the present study nine separate 30-day simulations were performed for both January (representing mid-summer conditions) and July (representing mid-winter conditions). The simulations were performed at a horizontal grid resolution of 60 km x 60 km using a domain of 100 x 100 grid points that covers sub-Saharan Africa. The monthly average of the nine simulations constitutes the model climatology for the month. The climatologies of rainfall and minimum and maximum temperature obtained in this manner are shown in Figure 1. Engelbrecht *et al.* (2002) illustrated that DARLAM is capable of simulating the regional characteristics of atmospheric variables like near-surface temperature, low-level wind patterns and rainfall over sub-Saharan Africa with considerable detail. The model does, however, tend to overestimate rainfall totals 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. It took approximately 11-minutes (CPU time) to simulate a model day at the specified model resolutions.

Predictive species modelling

We used a single predictive species modelling approach, originally developed by Jeffree & Jeffree (1994, 1996), for predicting species distribution patterns in the present study as a standardised base for evaluating the relative performance of the different climate data sets. This model was recently modified to accept multivariate inputs to yield probability of occurrence maps for species (Erasmus *et al.*, 2000). The original model was adapted to incorporate a variety of climatic predictor variables. Not only does this improve the original model, but it also allows the production of a probability surface of suitability for each species (Erasmus *et al.*, 2000), rather than merely a presence-absence distribution model. The multivariate predictive distribution modelling procedure developed by Erasmus *et al.* (2000) was employed throughout the current study. In short, this multivariate modelling approach uses the values of selected climate variables for each cell where a species had been recorded. These are plotted on an n-dimensional scatter plot (for the n-climate variables), and mean climate values subtracted to center values around the origin of the multidimensional scatter plot. An $n \times n$ covariance matrix is calculated and this matrix is used as an input to calculate eigen values and eigen vectors for the covariance matrix. These eigen vectors form the orthogonal principle axes of an n-dimensional hyperspace with the origin representing the theoretical core of the species' fundamental niche, as defined by the predictor climate variables (also see Robertson *et al*., 2001).

The climate variable values of all grid cells are then transformed into this eigen vector space. These transformed climate variables are subsequently divided by the eigen values and in the resulting *n*-dimensional hyperspace, the distance of any particular unsampled grid cell from the origin represents a measure of the suitability of that locality for the specific species (Robertson *et al*., 2001). According to Austin & Meyers (1996), the fundamental niche of an organism follows a broad Gaussian distribution. Such a Gaussian distribution is best approximated by a normal distribution but given that the distance from the origin of the hyperspace is calculated by the sum of the squared eigen vector axis scores, and that a squared normal distribution is equal to a chi-square distribution, the probability of any grid cell to be suitable for the selected species, can be read off a chi square probability table at the appropriate degrees of freedom (*m*, the number of climatic variables) (Robertson *et al*., 2001). The input data comprises 3000 grid cells covering sub-Saharan Africa populated with climate variables. Grid cells, in which particular tick species were recorded, are referred to as *known records* following Erasmus *et al*. (2002). Thus, on a scatter plot of climate variables (multivariate climate space), the values of climate variables from localities where species have been recorded are used to construct a confidence region where there is a high probability that the records reflect the core range of the species. Points falling within this confidence region are then mapped back to geographic space to represent an *interpolated distribution* (ID), represented as a probability of climate suitability (see Erasmus *et al*., 2000 for a detailed model description). Differences in model performance when employing a suit of different climate datasets were evaluated by comparing the interpolated species distributions.

Tick data

Point localities of recorded tick observations were obtained from Cumming (1999b). These data were compiled from various tick collections (see Cumming (1999b) for a detailed list of sources). Combining data sets from different sources invariably compounds identification and distribution errors and for this reason data congruence with Walker *et al.* (2000) were used to assess data quality. This later reference provides well-illustrated distributions of *Rhipicephalus* species. Synonyms provided in this reference also solve the common problem of referring to one species using two different names. The tick species selected for this study belong to the phylum Arthropoda, Class Arachnida and Family Ixodidae. Four species (*R. appendiculatus, R. capensis, R. longus* and *R. zambeziensis*) were selected from the 74 *Rhipicephalus* species found in Africa because their life history parameters and host preferences are relatively well known (Walker *et al.,* 2000). Tick point localities were assigned to particular 60km x 60km grid cells by means of a spatial intersect. A conservative estimate of the accuracy of these point localities is 0.2 degrees (Cumming, pers.comm.) and therefore this approximation is considered reasonable.

Climate variables

In the present study the climate variables employed were mean maximum temperature of January and July, mean minimum of January and July, and mean rainfall of January and July.

Comparison of interpolated species distributions across climate datasets.

Interpolated tick distributions emanating from the three climate data sets were compared by first calculating the true positive predictions (TP), that is the number of grid cells where the probability of climate suitability was equal or greater than 50% and where a tick had previously been recorded. The number of false negative (FN) predictions were also recorded, that is when the probability of climate suitability was less than 50% but where a tick had previously been recorded. The comparison among climate data sets was conducted using the proportional overlap method (Prendergast *et al.,* 1993; Lombard, 1995; Reyers *et al.,* 2000). Proportional overlap was calculated as TP / TP + FN where TP is the number of true positive predictions and FN + TP represents the number of negative plus the number of positive predictions, or, the maximum number of overlapping grid cells between observed and modeled tick distributions. This method was the most appropriate vehicle of comparison as absence data for tick distributions were not available. Although ROC analyses has been shown to be robust to the assumption of absence data in unsampled cells (Cumming, 2000a), the low prevalence of presence data (varying between 0.027 and 0.179) in this study means that ~2500 absence records would be added if this assumption was made. We are not confident that such a large change in the number of records can still yield robust model outputs. Therefore, in this case, the absence of absence data precludes the use of ROC analyses (Erasmus *et al.*, 2002).

Modelling random sub samples of known records

To evaluate the role played by tick dataset size on the performance of the climate datasets, we performed single random draws of varying percentages of the known tick distribution records without replacement (20%, 40%, 60%, 80%, 100% of known records). By varying the input dataset size and summing the proportional overlaps between predicted occurrences and known records across tick species, we were able to evaluate climate data performance for different levels of species data availability. A Kruskal-Wallis rank test between the proportional overlap values of the three climate data sets at every level of dataset reduction was performed (20%, 40%, 60%, 80& and 100%).

RESULTS

Comparing climate data sets

The observed variance in the CRES temperature data only becomes distance invariant after approximately 22 degrees, which is almost 3 times greater than that found for the DARLAM and CRU datasets (Fig. 2a). When the variogram is interpreted at the distance of reliability (Kaluzny *et al.*, 1998), which is half the maximum distance over the field of data for an experimental variogram, CRES data are still influenced by more remote data points, whereas the autocorrelation of CRU and DARLAM data have become distance invariant. This means that any particular value in the CRES data is more strongly influenced by data up to15 degrees away than either the CRU or DARLAM datasets where the sphere of influence is much more localized (~ 7 degrees). The relatively small number of observations used as inputs to create the CRES climate surface, forced interpolations over larger distances than for CRU, where more observational data were available for creating the climate surface. The slope of the curve for DARLAM temperature data appears to be steeper than the other curves over short distances (Fig. 2a). This illustrates how DARLAM, a process model, is very sensitive to topography and topographical features which are usually expressed over short distances, i.e. ~2 degrees. DARLAM's precipitation variogram (Fig. 2b) also displays a non-monotonic behaviour.

Interpolated tick distributions

The multivariate climate envelope model used in the present study provides probability of climate suitability values ranging from 0 - 1 across all grid cells. It was therefore necessary to select an appropriate probability level to use for comparison between the different species. In this study a 50% probability level of occurrence was used. This means that a tick was assumed present where the model predicted a probability of occurrence of ≥ 50% and the reverse. This follows a frequently employed convention in the field of predictive species modelling (Beard *et al.*, 1999; Brito *et al.,* 1999; Erasmus *et al.*, 2002; van Staden *et al.*, in press; also see Walker *et al.*, 1990 for even lower thresholds). When the proportion of the correctly predicted cases (true positives) were evaluated, it was found that in *R. appendiculatus*, a well-studied tick species, a true positive coverage of 70% (using DARLAM data) was obtained at a probability of occurrence level of ≥ 50%. This percentage of known records captured in the interpolated distribution is considered good, bearing in mind that the observed known records are not only determined by climate but also by the presence of suitable host species and other species specific micro-ecological or habitat selection factors which are not incorporated in this model.

The interpolated distribution for *R. appendiculatus* (Fig 3), when using any of the three datasets, was both visually and statistically broader than the extent of the known records, but the true positive predictions corresponded satisfactory with the known records (60%, 60% and 70% overlap using the CRES, CRU and DARLAM datasets respectively) (Table 1a, Fig. 4). There was a noteworthy positive congruence between the interpolated distributions and the known records in most areas of East, Central and Southern Africa: Uganda, Tanzania, Zambia, Zimbabwe and South Africa.

Unlike *R. appendiculatus* that is well studied and therefore presents a more comprehensive recorded distribution, the other tick species are poorly sampled and the actual distributions are still contested in the literature. While Walker *et al.* (2000) maintain that *R. capensis* is strictly South African; Cumming (1999b) reported it mainly in South Africa with some scattered records in Rwanda, DRC, Angola and Zambia (Fig. 3). The proportional overlap correlation between interpolated distribution and known records for *R. capensis* were 70%, 60%, and 60% for the CRES, CRU and DARLAM climate datasets respectively (Table 1b Fig.4). The highest overlap occurs in South Africa and Namibia with more than 90% of all true positive records found in RSA for the three climate data sets. This resultant interpolated distribution compares favorably with the Walker *et al.* (2000) distribution pattern and improves the suggested Cumming (1999b) distribution by eliminating a few scattered records in the north of South Africa and Namibia. The interpolated distributions of the other 2 tick species (Fig. 3) were also broader than the known records, with a 60%, 57% and 75% proportional overlap using CRES, CRU and DARLAM data for *R. longus* (Table 1c, Fig. 4) and 57%, 51%, and 62% for *R. zambeziensis* (Table 1d, Fig 4) respectively. One of the interesting and consistent results that emerged from these analyses is the ability of DARLAM to produce a higher proportion of true predictions across all species examined (Figs. 4 & 5).

Modelling random sub samples of known records

All three examined climate datasets seemed to be sensitive to the tick dataset size in terms of their ability to correctly predict tick distributions. However, DARLAM consistently performed better with higher degree of overlap between the interpolated distributions and known records (Figs. 5 & 6). Even with a 20% sub-sample of known records across the tick species, DARLAM was able to capture more than 50% of the known records and was consistently above 60% at higher levels of sub-sampling. However, none of these differences in proportional overlap reached statistical significance ($P < 0.05$) suggesting that DARLAM performs at least as well as any of the observed datasets.

DISCUSSION

Comparing spatial datasets

When interpreting the output of climate envelope based predictive species distribution models, it is necessary to take cognizance of differences in climate data that can be used as inputs. The datasets used in the present study represent 3 different types of climate data, namely: (i) observed data with variable coverage in space and time together with elevation influenced smoothing (CRES), (ii) better coverage and 30-year averaged observed data with elevation influenced smoothing (CRU), and (iii) purely process derived modeled climate data (DARLAM). Although some differences among the climate datasets are obvious, even to visual inspection (see Figures 1), a more quantitative measure of the difference in underlying climate parameters was obtained by comparing omnidirectional variograms (Kaluzny *et al.,* 1998; Rossi *et al.,* 1992; Nielsen & Wendroth, 2001) for these data sets. In a variogram the variance of the property being measured, i.e. rainfall or temperature, is statistically expressed as a function of the distance between observations within a given spatial domain, i.e. sub-Saharan Africa (Nielsen & Wendroth, 2001). The difference between pairs of observations separated by a specific distance is plotted and the slope, position and shape of this graph gives an indication of the scale at which the underlying processes might operate. These variograms can therefore be interpreted as a measure of the degree of difference between the various datasets. For example, the emergence of non-monotonic behaviour in the DARLAM dataset (Fig. 2b) is indicative of spatial variation at scales other than the sampling units (Nielsen & Wendroth, 2001). Given the fact that precipitation is the result of complex atmospheric interactions at different scales, such a non-monotonic variogram can be expected from a process-based model such as DARLAM. In the analyses conducted here, the CRES dataset varied over larger spatial scales than either the CRU or DARLAM datasets. Thus, the three data sets used in this study do not only appear different to a casual visual inspection (Fig. 1), but are also different with respect to the spatial dependencies of database characteristics which influence adjacent climate values (Fig. 2).

Model evaluation

Usually the validity of a predictive species distribution model is assessed by its ability to predict both negative and positive cases (Fielding & Bell, 1997). However, the opportunistic manner in which the tick distribution data were collected precludes rigorous model evaluation. This is as true absence data are not available for these species, mainly because some areas were simply poorly sampled (Fig. 3). This same climate envelope model was however previously 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 model performance using receiver operator characteristic analyses (Fielding & Bell, 1997). The model performed significantly better than a random model with no discriminatory ability. The model 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). In sum, the model performed satisfactorily and is therefore considered adequate for the purposes of the present study.

Predicting tick distributions

At the outset it is important to acknowledge that, although we use a climate envelope approach in this study, we are not suggesting that this is an adequate basis for predicting the fine scale distributions of tick species across the African continent. Tick distributions and abundances are likely to be impacted by factors other than climate, such as host abundance, host resistance to ticks, acaricide use and grazing management (see

Cumming, 1998, 1999a, 2002). Most of these changes interact with temperature and rainfall regimes and in the absence of experimental data. It is impossible to separate the effects of these interrelated factors. This, compounded by the fact that the broad scale ecology of only a few tick species have been studied in detail (Cumming, 2002), means that employing climate variables as the main limiting factors for tick distributions remains the best option available. Minimum temperature, maximum temperature and rainfall have similar predictive abilities to one another; when considered together; their predictive ability increases substantially (Cumming, 2002). This is probably a consequence of their being correlated with one another. The intimate relationship between climate and tick distributions has also been reported elsewhere (Rechav, 1981; Minshull & Norval, 1982; Walker, 1974; Walker *et al.*, 2000). Taken in the context of current knowledge, we agree with Cumming (1999a) that the direct effects of climate typically determine the distributions of African ticks, but that biotic variables such as vegetation type and host distributions, may be important in creating heterogeneity in tick distributions at finer scales (Minshull & Norval, 1982) and play a subordinate role in limiting the species ranges of ticks at broad spatial scales (Cumming, 2002).

Against this background we proceeded to employ distribution data from a number of tick species that are considered sound taxa and that are widely collected. This was to evaluate the use of three different climate datasets for carrying out predictive species distribution modelling. These datasets varied in terms of the manner in which they were generated. Two datasets (CRES and CRU) represented the traditionally used datasets (see Guisan & Zimmermann, 2000; Robertson *et al.,* 2001; Erasmus *et al.,* 2002) for this type of predictive modelling activity. These are based on observed climate data and were subsequently interpolated to generate climate surfaces for the continent (Hutchinson, 1991; Hutchinson & Gessler, 1994; McMahon *et al.*, 1995; Hutchinson *et al.*, 1996; New *et al.,* 1999). The third dataset was derived from a nested limited-area model, is entirely based on a simulation of climate processes and does not use any observed meteorological data to generate climate surfaces (DARLAM - Engelbrecht *et al.,* 2002). In all instances explored here, cross species and degrees of data sub-sampling, the DARLAM dataset was equal to or marginally outperformed the interpolated climate surfaces in predicting the distributions of species. This suggests that process-based modeled datasets, such as DARLAM, should in the future be considered viable or even preferred datasets for modelling the predicted distributions of species, especially when considering their ability to capture climate at fine scales relative to range sizes of species.

A further advantage of employing process-based modeled climate surfaces for predicting species distributions is that this provides improved compatibility when using these predictions as a basis for exploring the consequences of climate change for future species distributions. This improved compatibility flows from the fact that future climate surfaces can easily be generated from nested limited-area models such as DARLAM. Thus, we can easily model the future using similar process-based models as used here in DARLAM but, in contrast, we cannot observe the future in order to generate climate datasets for direct comparison with the observed data derived climate datasets (CRES and CRU).

In conclusion, the recent availability of high-resolution nested limited-area models (DARLAM – Engelbrecht *et al.*, 2002) now means that there are alternative climate surfaces available for modelling species distributions at broad scales. The results obtained here suggest that the use of data derived from a nested limited-area or process model for predicting species distributions, offer a viable and even a preferred alternative to using interpolated climate surfaces derived from observed climate data. This is especially true when the spatial and temporal coverage of observed datasets are poor, resulting in climate data surfaces that are strongly spatially autocorrelated over large distances.

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References

Austin, M. P. & Meyers, J. A. (1996) Current approaches to modelling the environmental niche of eucalyts: Implications for management of forest biodiversity. *Forest Ecological Management*, **85**, 95-106.

Beard, K. H., Hengartner, N. & Skelly. D. K. . (1999). Effectiveness of predicting breeding bird distributions using probabilistic models. *Conservation Biology*, **13**, 1108-1116.

Brito, J. C., Crespo, E. G., & Paulo, O. S.(1999) Modelling wildlife distributions: logistic multiple regression vs overlap analysis. *Ecography,* **22**, 251-260.

Coakley, S. M., Scherm, H. & Chakraborty, S.,(1999) Climate Change and plant disease management. *Annual Review of Phytopathology*, **37**, 399-426.

Cumming, G. S. (1998) Host preference in African Ticks (Acari: Ixodidae): a quantitative data set. *Bulletin of Entomological Research,* **88,** 379-406.

Cumming. G. S. (1999a) Host distributions do not limit the species ranges of most African Ticks (Acari: Ixodida). *Bulletin of Entomological Research,* **89,** 303 - 327.

Cumming, G.S. (1999b) *The evolutionary ecology of African ticks.* Unpublished Dphil thesis, University of Oxford, Oxford, UK.

Cumming, G.S. (2000a) Using between-model comparisons to fine-tune linear models of species ranges. *Journal of Biogeography*, **27**, 441-455.

Cumming, G. S. (2000b) Host use does not clarify the evolutionary history of African ticks (Acari: Ixodida). *African Zoology,* **35,** 43-50.

Cumming. G.S. (2002) Comparing climate and vegetation as limiting factors for species ranges of African ticks. *Ecology*, **83** (1), 255-268.

Davies H. C. (1976) A Lateral boundary formulation for multilevel prediction models. *Quarterly Journal of the Royal Meteorology Society*, **102**, 405-418.

Engelbrecht, F.A., Rautenbach, C.J. deW., McGregor, J.L. & Katzfey, J.J. (2002) January and July climate simulations over the SADC region using the limited-area model DARLAM. *Water SA*, **28**, 361-373.

Erasmus B.F.N, Kshatriya, M., Mansell, M.W., Chown, S.L & van Jaarsveld, A.S. (2000) A modelling approach to antlions (Neuroptera: Myrmeleontidae) distribution patterns. *African Entomology,* **8**,157-168.

Erasmus, B.F.N., van Jaarsveld, A.S., Chown S.L., Kshatriya, M & Wessels, K.J. (2002). Vulnerability of South African animal taxa to climate change. *Global Change Biology,* **8**, 679-693.

Fielding A.H.& Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* **24**, 38-49.

Guisan A.& Zimmerman N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling,* **135**, 147-186.

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S. Dobson, A. P., Ostfeld, R. S. & Samuel M. D. (2002) Climate warming and disease risk for terrestrial and marine biota. *Science*, **296**, 2158-2162.

Horak, I. G. Potgieter, F. T.,Walker, J. B., De Vos, V. & Boomker, J.(1983) The Ixodid tick burdens of various large ruminant species in South African nature reserves. *Onderstepoort Journal of Veterinary Research*, **50**, 221-228.

Horak, I. G., Boomker, J. & Flamand, J. R. B. (1995) Parasites of domestic and Wild animals in south Africa. XXXIV. Arthropod parasites of nyalas in northeastern Kwazulu-Natal. *Onderstepoort Journal of Veterinary Research,* **62**, 171-179.

Hutchinson, M.F. (1989) A new procedure for gridding elevation and streamline data with automatic removal of spurious pits. *Journal of Hydrology,* **106**, 211-232.

Hutchinson, M.F. (1991) The application of thin plate splines to continent-wide data assimilation. *Data Assimilation Systems* (ed. J.D. Jasper), pp. 104-113. BMRC Research Report No 27, Bureau of Meteorology, Melbourne, Australia.

Hutchinson, M.F. & Gessler, P.E. (1994) Splines - more than just a smooth interpolator. *Geoderma,* **62**, 45-67.

Hutchinson, M. F., Nix, H. A., MacMahon, J. P. & Ord, K. D. (1996) A topographic and climatic database for Africa- Version 1.1. Australian National University, Canberra.

Jeffree E.P.& Jeffree C.E. (1994) Temperature and the biogeographical distribution of species. *Functional Ecology,* **8**, 640-650

Jeffree C.E.& Jeffree E.P. (1996) Redistribution of the potential geographical ranges of Mistletoe and Colorado Beetle in Europe in response to the temperature component of climate. *Functional Ecology,* **10**, 562-577.

Kaluzny S.P., Vega S.C., Cardoso T.P. & Shelly A A. (1998) *S+ Spatial Stats – User's manual for Windows® and Unix®* Springer-Verlag, New York.

Lombard, A.T. (1995). The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide?. *South African Journal of Zoology*, **30**, 145-163.

McGregor, J.L. (1993) Economical determination of departure points for semi-Lagrangian Models. *Monthly Weather Review*, **121**, 221-230.

McGregor, J.L. (1997) Regional climate modelling. *Meteorology & Atmospheric Physics* **63**, 105-117.

McMahon, J.P., Hutchinson, M.F., Nix, H.A. and Ord, K.D. (1995) *ANUCLIM User's Guide*. Draft Report, Centre for Resource and Environmental Studies, Australian National University, Canberra, Australia.

Mesinger, F. & Arakawa, A. (1976) Numerical Methods Used in Atmospheric Models. GARP Publications Series 17. Vol. 1, WMO, 66 pp.

Messenger, P. S. (1959) Bioclimatic studies with insects. *Annual Review of Entomology*, **4**, 183-206.

Meats, A. (1989) Bioclimatic potential. *Fruit flies: their biology, natural enemies and control* (ed. By A. S. Robinson & G. Hooper) 3B, pp241-252. Elsevier, Amsterdam.

Minshull, J.I. & Norval, R.A.I. (1982) Factors influencing the spatial distribution of *Rhipicephalus appendiculatus* in Kyle recreational park, Zimbabwe. *South African Journal of Wildlife Research*, **12**, 118-123.

New, M., Hulme, M. & Jones, P. (1999) representing twentieth-century space-time climate variability. Part I: Development of a 1961-90 mean monthly terrestrial climatology .*Journal of Climate*, **12**, 829-856.

Nielsen, D & Wendroth, O. (2001) *Spatial and Temporal Statistics - Sampling Field Soils and Their Vegetation*. Catena-Verlag, New York.

Norval, R. A. I., Walker Jane B. & Colborne J. (1982) The Ecology of *Rhipicephalus zambeziensis* and *Rhipicephalus appendiculatus* (Acarina, Ixodidae) with particular reference to Zimbabwe. *Onderstepoort Journal of Veterinary Research,* **49,** 181-190.

Perry, B. D., Lessard, R. A. I., Norval, R. A. I.., Kundert K. & Kruska R.(1990) Climate, vegetation and the distribution of *Rhipicephalus appendiculatus* in Africa. *Parasitology Today,* **6,** 100-104.

Phillips N. A (1957) A coordinate system having some special advantages for numerical forecasting. *Journal of Meteorology,* **14,** 184-185.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335-337.

Randolph (2001)The shifting landscape of tick-borne zoonoses: tick-borne encephalitis and Lyme borreliosis in Europe. *Philosophical Transactions of the Royal Society, London* B, **356**, 1045-1056.

Randolph (2002) Ticks and Tick-borne disease systems in space and from space. *Advances in Parasitology*, **47**, 217-243.

Randolph, S.E. & Rogers, D. J. (1997) A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology,* **115,** 265-279.Randolph, S. E. and Rogers, D. J. (2000) Fragile transmission cycles of tick-borne encephalitis virus may be disrupted by predicted climate change. *Proceedings of the Royal Society, London* B, **267**, 1741-1744.

Rechav, Y. 1981 Ecological factors affecting the seasonal activity of the brown ear tick Rhipicephalus appendiculatus. *Tick Biology and control* (ed. by G. B. Whitehead and J. D. Gibson) pp. 187-191. Tick Research Unit, Rhodes University, South Africa.

Reyers, B., van Jaarsveld, A.S. & Krüger, M. (2000) Complementarity as a biodiversity indicator strategy. Proceedings of the Royal Society, London B, **267**, 505 – 513.

Robertson, M.P., Caithness, N. & Villet, M.H. (2001) A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. *Diversity and Distributions,* 7,15-27.

Rogers, D. J. & Randolph S. E. (1993) Distribution of tsetse and ticks in Africa: Past, Present and future. *Parasitology Today,* **9**, 266-271.

Rogers & Randolph (2000) The global spread of malaria in a future warmer world. *Science*, **289**, 1763-1766.

Rossi RE, Mulla DJ, Journel JG, Frantz EH. (1992) Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecological Monographs,* **62**, 277-314.

Short, N. J. & Norval, R. A. I. (1981) The Seasonal activity of *Rhipicephalus appendiculatus* Neumann 1901 (Acari: Ixodidae) in the high veld of Zimbabwe Rhodesia. *Journal of Parasitology,* **67**, 77-84.

Sutherst & Maywald (1985) A computerized system for matching climates in ecology. Agriculture, Ecosystem and Environment, **13**, 281-299.

Sutherst , R. W., Mayward, G. F. & Skarratt, D. B. (1995) Predicting insect distribution in a changed climate. *Insects in a changing environment* (ed. By R. Harrington and N. E. Stork), pp. 59-91.

Tukahirwa, M. E. (1976) The Effects of temperature and relative humidity on the development of *R. appendiculatus* Neumann (Acari, Ixodidae). *Bulletin of Entomological Research*, **66**, 301-312.

Van Staden, V., Erasmus, B.F.N., Roux, J., Wingfield, M.J., and van Jaarsveld A.S. (in press) Modelling the spatial distribution of two important South African plantation forestry pathogens *Forest Ecology and Management*

Walker, P. A. (1990). Modelling wildlife distributions using a geographic information system: kangaroos in relation to climate. *Journal of Biogeography*, **17**: 279-289

Walker, J. B. (1974)*The Ixodid ticks of Kenya. A review of present knowledge of their hosts*. London: Commonwealth Institute of Entomology.

Walker, J.B, Keirens E. J. and Horak, I. G. (2000) The Genus *Rhipicephalus* (Acari, Ixodidae)*: A guide to the brown ticks of the world*. United Kingdom: Cambridge University Press.

Walsh, K. & McGregor, J.L. (1995) January and July climate simulations over the Australian region using a limited-area model. *Journal of Climate*, **8**, 2387-2403.

Table 1: The number of true and false predictions generated for four different tick species by a predictive species distribution model (Erasmus *et al.* 2002) using different climate datasets (CRES, CRU, DARLAM) and complete species datasets. KR = known records, TP = true positive predictions, FN = False negative predictions.

(a) Rhipicephalus appendiculatus			
	CRES	**CRU**	**DARLAM**
KR	538	538	538
TP	315	320	372
FN	223	217	166
Proportional overlap (TP/TP + FN)	**60%**	**60%**	**70%**
(b) R. capensis			
KR	189	189	189
TP	128	119	108
FN	60	70	81
Proportional overlap	**60%**	**60%**	**57%**
(c) R. longus			
KR	129	129	129
TP	78	74	97
FN	51	55	32
Proportional Overlap	**60%**	**56%**	**75%**
(d) R. zambeziensis			
KR	82	82	82
TP	47	42	51
FN	35	40	31
Proportional Overlap	**60%**	**50%**	**65%**

FIGURE LEGENDS

FIGURE 1. Maximum temperature (deg C) and rainfall (0.1mm/day) for January and July as represented by three climate datasets (CRES, CRU and DARLAM) (a) Mean maximum temperature for January, (b) mean maximum temperature for July, (c) mean rainfall for January and (d) mean rainfall for July

FIGURE 2a. Variogram of January maximum temperature across sub Saharan Africa for the CRES, CRU and DARLAM data sets. Distance is measured in geographical degrees. Spatial dependence (gamma) is calculated following Nielsen & Wendroth (2001).

FIGURE 2b. Variogram of January rainfall across sub Saharan Africa for the CRES, CRU and DARLAM data sets. Distance is measured in geographical degrees. Spatial dependence (gamma) is calculated following Nielsen & Wendroth (2001).

FIGURE 3. Recorded known records (KR) and interpolated distributions (ID) of ticks obtained using species predictive modelling based on each of the three climate datasets (CRES, CRU and DARLAM) (a) *R. appendiculatus*, (b) *R. capensis*, (c) *R. longus*, (d) *R. zambeziensis*.

FIGURE 4. Known records (KR) and true predictions (TP) for all tick species generated for each climate dataset (a) *R. appendiculatus*, (b) *R. capensis*, (c) *R. longus*, (d) *R. zambeziensis*.

FIGURE 5. Degree of proportional overlap between known records and predicted presence of all tick species for each climate dataset. These proportional overlap values were calculated at different levels of random sub-sampling of

known records (a) *R. appendiculatus*, (b) *R. capensis*, (c) *R. longus*, (d) *R. zambeziensis*

FIGURE 6. Mean value of proportional overlap (mean ± s.d) across all tick species at different levels of random sub-sampling of known records . This analysis is repeated for each climate dataset.

Figure 1

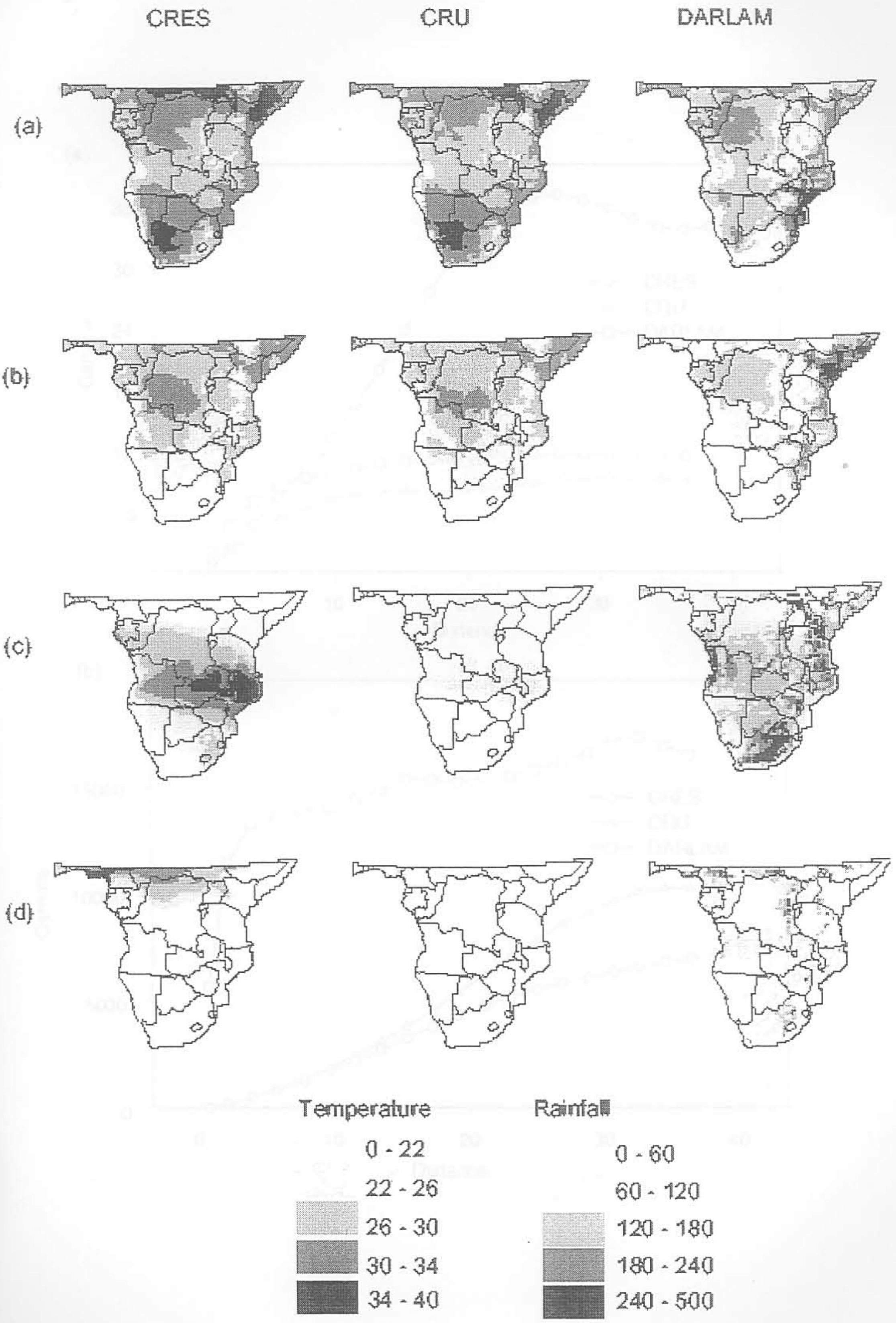

CRES
CRU
DARLAM
(a)
(b)
(c)
(d)
Temperature
0 - 22
22 - 26
26 - 30
30 - 34
34 - 40
Rainfall
0 - 60
60 - 120
120 - 180
180 - 240
240 - 500

Figure 2

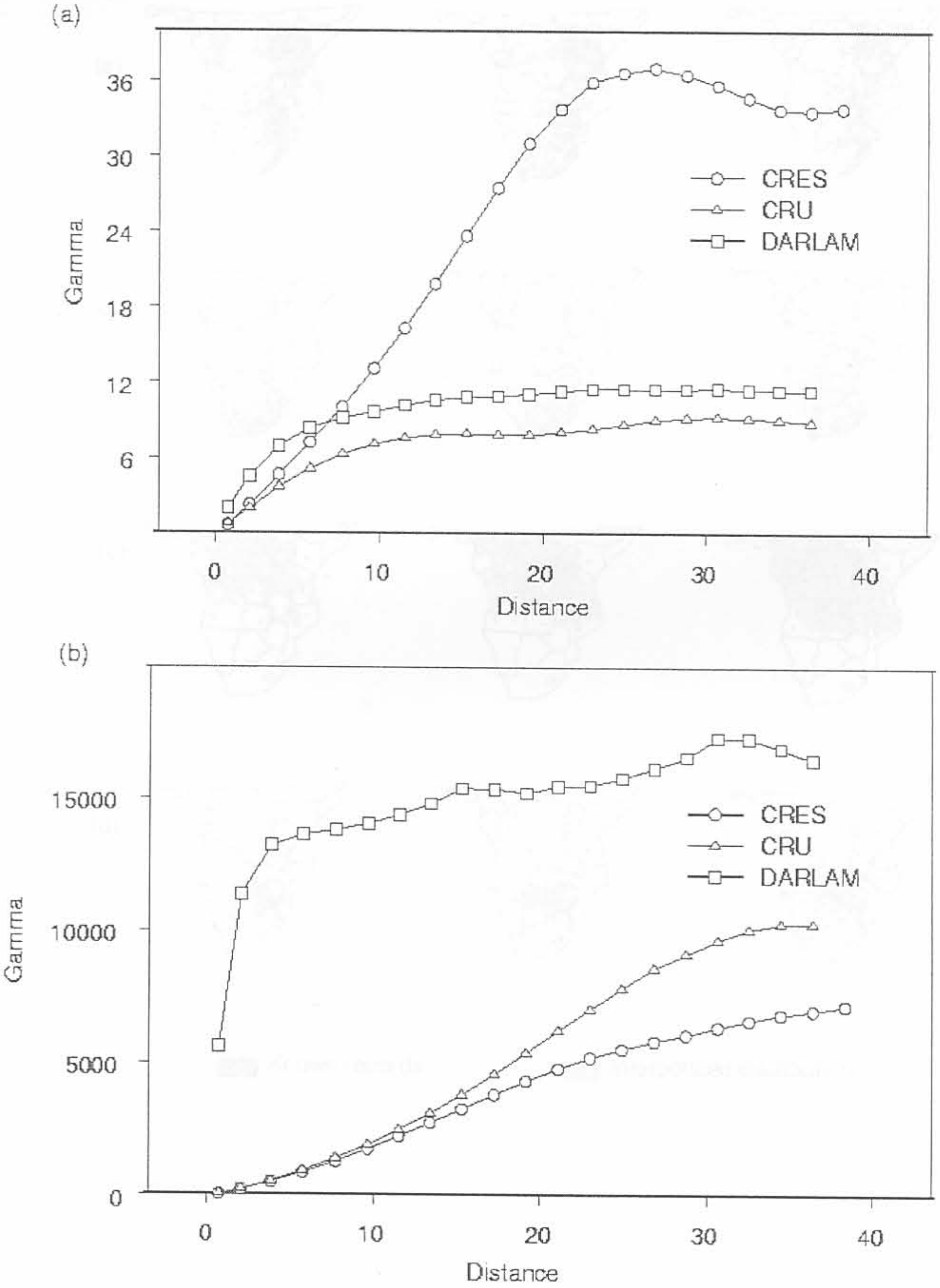

(a)
Gamma
36
30
24
18
12
6
0
10
20
30
40
Distance
CRES
CRU
DARLAM
(b)
Gamma
15000
10000
5000
0
0
10
20
30
40
Distance
CRES
CRU
DARLAM

Figure 3

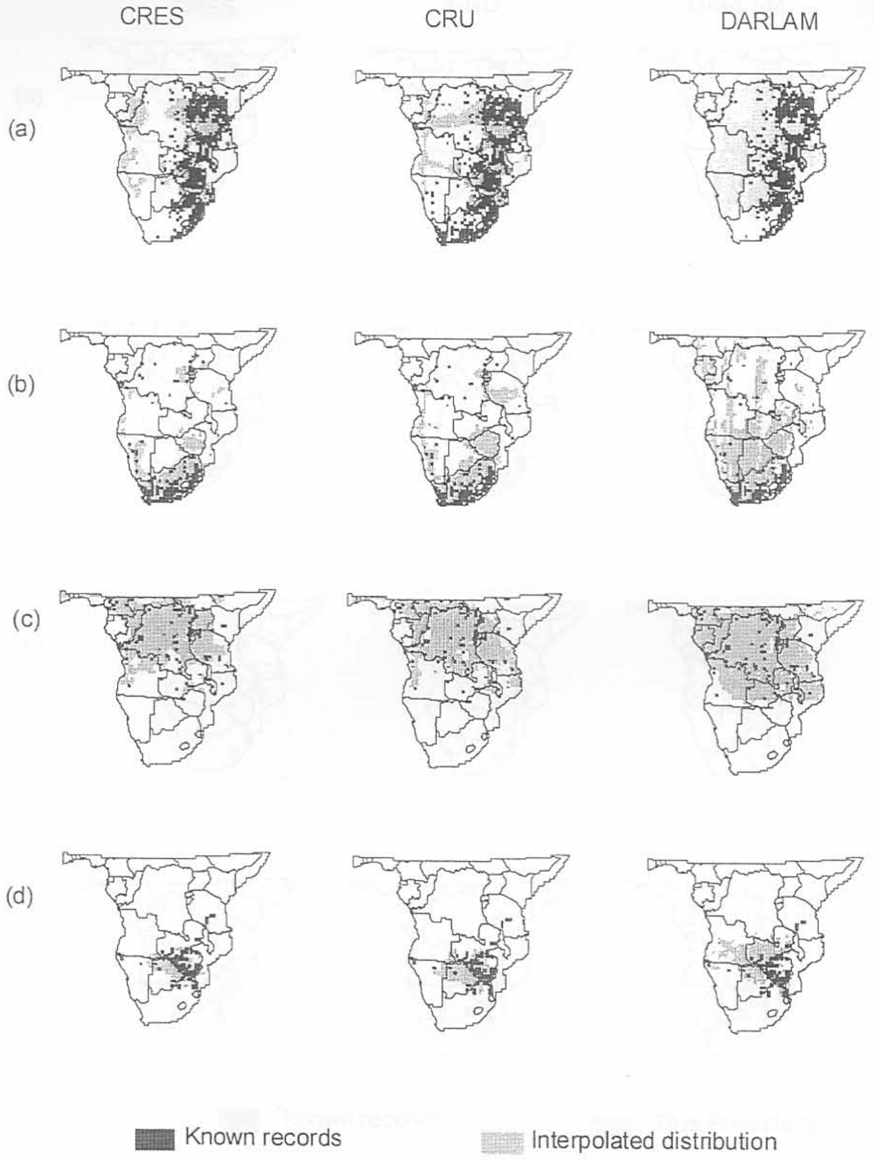

CRES
CRU
DARLAM
(a)
(b)
(c)
(d)
Known records
Interpolated distribution

Figure 4

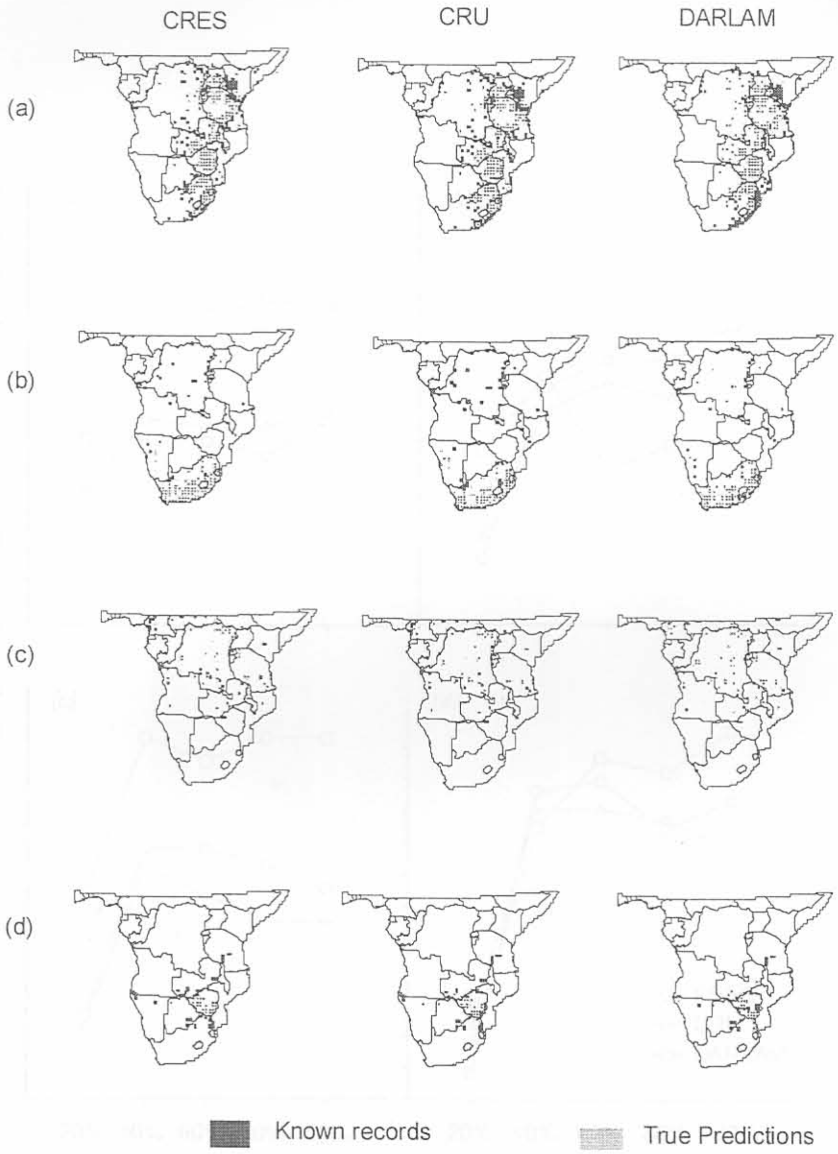


Figure 5

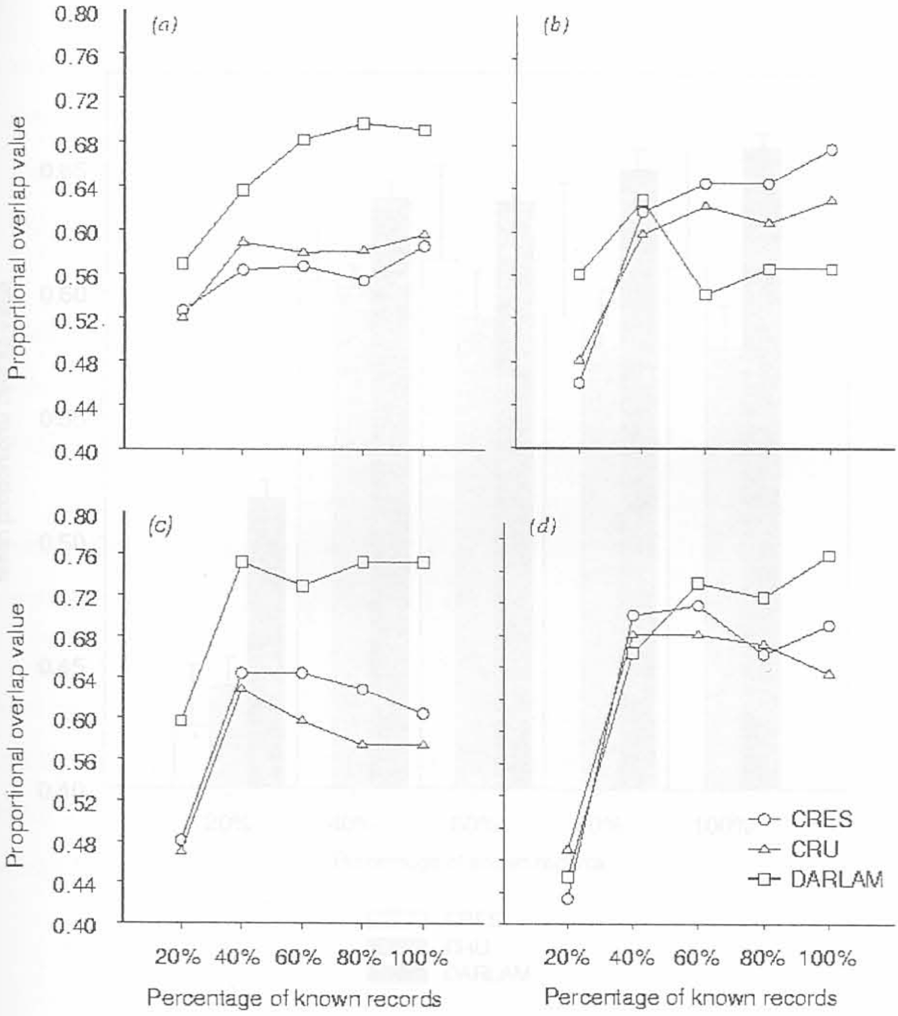
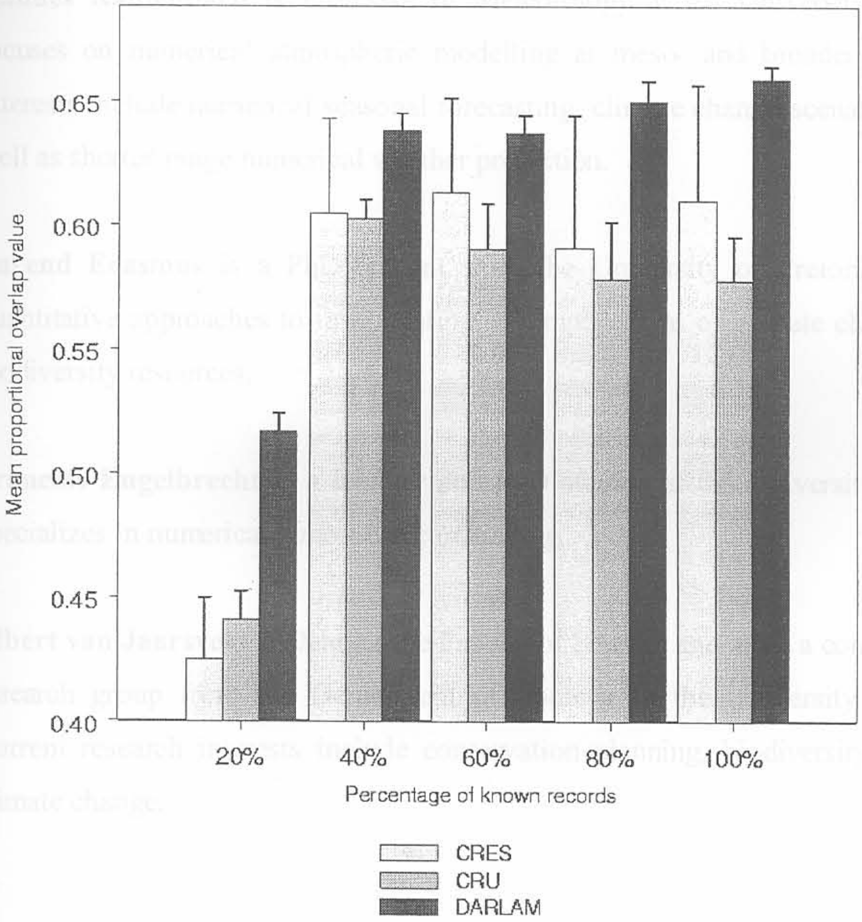

(a)
(b)
(c)
(d)
Proportional overlap value
0.80
0.76
0.72
0.68
0.64
0.60
0.56
0.52
0.48
0.44
0.40
20% 40% 60% 80% 100%
Percentage of known records
CRES
CRU
DARLAM

Figure 6


Mean proportional overlap value
0.40
0.45
0.50
0.55
0.60
0.65
20%
40%
60%
80%
100%
Percentage of known records
CRES
CRU
DARLAM

BIOSKETCHES

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