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Using potential distributions to explore environmental correlates of bat species richness in southern Africa: effects of model selection and taxonomy

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Abstract We tested the prediction that at coarse spatial scales, variables associated with climate, energy, and productivity hypotheses should be better predictor(s) of bat species richness than those associated with environmental heterogeneity. Distribution ranges of 64 bat species were estimated with niche-based models informed by 3629 verified museum specimens. The influence of environmental correlates on bat richness was assessed using ordinary least squares regression (OLS), simultaneous autoregressive models (SAR), conditional autoregressive models (CAR), spatial eigenvector-based filtering models (SEVM), and Classification and Regression Trees (CART). To test the assumption of stationarity, Geographically Weighted Regression (GWR) was used. Bat species richness was highest in the eastern parts of southern Africa, with a concentration of hotspots in central Zimbabwe and Mozambique. We found support for the predictions of both the habitat heterogeneity and climate/productivity/energy hypotheses, and as we expected, support varied among bat families and model selection. Richness patterns and predictors of *Miniopteridae* and *Pteropodidae* clearly differed from those of other bat families. Altitude range was the only independent variable that was significant in all models and it was most often the best predictor of bat richness. Standard coefficients of SAR and CAR models were similar to those of OLS models, while those of SEVM models differed. Although GWR indicated that the assumption of stationarity was violated, the CART analysis corroborated the findings of the curve-fitting models. Our results identify where additional data on current species ranges, and future conservation action and ecological work are needed [*Current Zoology* 58 (): –, 2013].

Key words Chiroptera, Macroecology, Niche-based models, Spatial models, Species richness

One of the most universal features of global biodiversity is the variability of species richness across different regions. Some regions harbour a high proportion of diversity, while others are almost devoid of species, and most

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exhibit intermediate diversity (Gaston and Blackburn, 2000). Notwithstanding burgeoning human-induced habitat loss and climate change, understanding the drivers of species richness is central to ecology and evolutionary biology. Accordingly, there has been much progress in developing robust analytical techniques to predict species distributions (Guisan and Thuiller, 2005; Tsoar et al., 2007) and control for spatial autocorrelation (Dormann et al., 2007; Kissling and Carl, 2008; Bini et al., 2009). Currently, there appears to be consensus that variables related to ambient-energy, productivity, current climatic conditions and habitat heterogeneity constitute the dominant controls over assemblage attributes and species distributions at broad spatial scales (Field et al., 2009). However, the relative importance of these and other factors, and the ubiquity of factors across biogeographic regions and taxonomic groups are still under scrutiny. Furthermore, non-spatial and spatial models may (or may not) substantially differ in the rank and importance of regression coefficients (Bini et al., 2009). More specifically, standardized regression coefficients from curve-fitting methods have been widely used to evaluate the relative importance of explanatory variables and to test hypotheses about drivers underlying these patterns, despite the extensive body of literature cautioning the exclusive use of these methods (Hawkins, 2012).

To further complicate matters, closely related taxa often respond differently to environmental factors, probably the result of constraints associated with the historical diversification of lineages (Ricklefs, 1987; 2004). Among small mammals in the New World for example, the effects of energetic constraints was the most significant correlate of bat species richness, while habitat heterogeneity was strongly associated with richness of rodents and artiodactyls (Ruggiero and Kitzberger, 2004). By contrast, the most important predictor of insectivore, climber and carnivores/omnivore richness in southern Africa was found to be woody plant richness, but for bat richness the best predictors were annual precipitation and actual evapotranspiration (Qian et al., 2009). In fact, the wide range of life history traits and roosting behaviours in bat families (Bernard and Cumming, 1997; Monadjem et al., 2010a) should result in the association between richness patterns and environmental correlates differing at the family level (Patten, 2004), but this remains to be tested in the Old World.

Issues of data quality are critical ingredients in these debates. It is becoming increasingly clear that the attributes and quality of the distribution data significantly influence outcomes of models seeking to elucidate underlying determinants of richness patterns (Hurlbert and White, 2005; Graham and Hijmans, 2006; McPherson and Jetz, 2007). Ideally, species richness data are systematically collected with a constant sampling effort at selected study sites. However, this approach is difficult for most taxa particularly at broad spatial scales. Consequently, distributional data for taxa are typically collated from a variety of available sources, and species ranges are demarcated by drawing a polygon around known occurrences to generate maps reminiscent of field-guides. A more promising approach is represented by the emerging trend to model the potential distributions of individual species, informed primarily by georeferenced records and algorithms employing environmental variables to estimate niche boundaries of the species' entire range envelope (Jiménez-Valverde et al., 2010). Assuming that taxonomic and spatial inaccuracies, as well as biases in the spatial coverage of the data can be controlled for (Graham et al., 2004), these modelled distribution maps represent a useful tool for investigating broad-scale richness patterns and the dynamics between species richness and climate (Vasconcelos et al., 2011).

In this study we tested the hypothesis that at broad spatial scales, variables associated with climate, productivity and energy hypotheses should have a stronger influence on bat species richness than those associated with environmental heterogeneity hypotheses (Field et al., 2009). We estimated bat richness gradients in southern Africa by overlaying the potential range maps of individual bat species predicted by niche-based models, which were informed by verified

museum records. We expected that the importance of environmental correlates of richness would vary with respect to taxonomy (order and family levels) and model selection (non-spatial versus spatial models, curve-fitting versus machine-learning methods).

Our choice of correlates does not mean that we are unaware that climate/productivity/energy and habitat heterogeneity are only two classes of explanatory variables of species richness. Rather, we reasoned that while other correlates, such as human land use (Chown, 2010) and biotic interactions (Qian et al., 2009) are likely to influence the current geographical distribution of taxa, predicted distribution patterns of taxa informed primarily by museums specimens collected over 50 years should primarily reflect climate/productivity/energy and to a lesser degree habitat heterogeneity variables operating at broad spatial scales. Nonetheless, we acknowledge that a full understanding of the drivers of bat species richness in the region is unlikely to be achieved without additional investigations. These include the understanding of the relative influence of different types and combinations of environmental variables at various spatial scales, and incorporating occurrence data from other sources such as acoustic monitoring of bat echolocation calls (Walters et al., 2012). However, the approach we use provides an initial best estimate of expected bat richness gradients and correlates assuming minimum influence of humans and other biotic processes, and how these vary with respect to taxonomy and model selection. This estimate can be used as a broad guide to identify pertinent conservation action and ecological work, while additional, more specific data on current species ranges and their change under different land use and climate scenarios are collected.

1 Materials and Methods

1.1 Study area

Our study area covers the southern third of the African continent south of 8°S. Excluding the political region of Tanzania, this includes Angola, Zambia, Malawi, Mozambique, Swaziland and South Africa. This region is highly varied in climate, topography, altitude and habitat structure. There is an east-west aridity gradient from the humid coastal plains of Mozambique to the Namib Desert in the west. There is also a north-south gradient resulting in decreasing temperature with increasing distance from the equator. The greater extent of southern and central Africa comprises a vast elevated plateau (average 1,000 m asl) with flanking escarpments. In the east the Maluti - Drakensberg and Mpumalanga mountains of South Africa extend to the Zimbabwe's Chimanimani highlands, with the Angolan and Namibian escarpments in the west. Moreover, coastal plains and principal drainage basins (Cuanza, Kunene, Limpopo, Orange, and Zambezi) alongside other distinct regions of relief contribute to the geomorphic heterogeneity of this region. The region comprises a diverse habitat mosaic representing nine biomes including gallery forest, savanna, open grassland and desert. For further details see Monadjem et al. (2010a).

1.2 Modelling species distributions

Because there are challenges inherent to using museum data (Graham et al., 2004), we compiled georeferenced locality data of bat species from museum specimen records that were physically checked by the authors for taxonomic and spatial inaccuracies (Monadjem et al., 2010a). Because sampling bias and intensity (Robertson et al., 2010; Botts et al., 2011) can strongly influence model output and result in overfitting, we included only locality data that were greater than 10 km apart (Dixon, 2011). To make the database relevant to the timeframe of the bioclimatic variables used in the niche-based modelling (see below), we excluded records that were collected before 1960. Given that niche models

perform poorly for species with a small number of occurrences (Stockwell and Peterson, 2002), we also excluded species with < 10 occurrence records. It is notable that most of the excluded species are marginal to the region showing distribution patterns that extend only into the northern-most parts of central and southern Africa. These include *Casinycteris argynnis*, *Epomophorus anelli*, *E. grandis*, *Epomops franqueti*, *Hypsignathus monstrosus*, *Megaloglossus woermanni*, *Micropteropus intermedius*, *Myonycteris torquata*, *Plerotes anchietae*, *Rousettus lanosus* (Pteropodidae), *Rhinolophus alcyone*, *R. eloquens* (Rhinolophidae), *Lavia frons* (Megadermatidae), *Saccolaimus peli* (Emballonuridae), *Nycteris arge*, *N. intermedia*, *N. major*, *N. nana* (Nycteridae), *Chaerephon major*, *Mops brachypterus*, *M. nanulus*, *M. thersites*, *Myotis whitleyi* (Molossidae), *Miniopterus minor* (Miniopteridae), *Glauconycteris argentata*, *G. beatrix*, *Mimetillus moloneyi*, *Neoromicia tenuipinnis*, and *Pipistrellus nanulus* (Vespertilionidae). Specimen records for the remaining species excluded from the dataset, e.g. *Lissonycteris goliath*, *Myonycteris relicta* (Pteropodidae), *Rhinolophus deckenii*, *R. maendeleo*, *R. sakejensis* (Rhinolophidae), *Coleura afra* (Emballonuridae), *Tadarida ventralis* (Molossidae), *Laephotis wintoni*, *Neoromicia cf. melckorum*, *Pipistrellus grandidieri*, and *Scotophilus nigrita* (Vespertilionidae), comprised few verified and/or unverified records typically in areas of high bat species richness. Thus, our database used in the niche-based modelling comprised occurrence records of well-established resident bat species in the region.

Because the database comprised verified occurrence data but not accurate absence data, distribution ranges of species were modelled using Maxent (version 3.1.0; Phillips and Dudík, 2008). Maxent finds the probability distribution of maximum entropy (the distribution that is most spread-out, or closest to uniform) subject to the constraints imposed by the information available from the observed occurrence of the species and environmental conditions across the study area. This probability is represented as a map depicting the species' expected range. Maxent has performed well in comparison to other niche modelling approaches (Elith et al., 2006; Wisz et al., 2008). We selected nine 2.5 arc-minutes (~5 km) resolution BIOCLIM variables from the WorldClim database (Hijmans et al., 2005) - annual mean temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of the wettest month (BIO13), precipitation of the driest month (BIO14) and precipitation seasonality (BIO15) – because these climatic variables have been found to be highly related to the ecological and physiological tolerances of organisms, and thus effective at predicting the distribution ranges of species using Maxent (Hijmans and Graham, 2006). Importantly, previous studies have shown that these proximal variables are functionally effective predictors of bat distribution ranges (e.g. Rattrimomanarivo et al., 2009, Monadjem et al., 2010a, Dixon, 2011, Flanders et al., 2011, Stoffberg et al., 2012). We did not include distal predictors such as elevation because they rarely influence the prediction of distribution range (Elith and Leathwick, 2009). Moreover, Maxent implicitly performs model selection, and using a model selection procedure such as stepwise regression to choose variables can worsen the performance of the model (Elith et al., 2010). The models were run with the convergence threshold set to 10^{-5} , the maximum number of iterations set to 1000, the regularization multiplier set to 1, and models were calibrated using both linear and quadratic features. We selected the logistic output format that yields continuous values ranging from 0 to 1 indicating the probability of suitable environmental conditions. The distribution maps were converted into binary presence absence maps with equal training sensitivity and specificity threshold (Liu et al., 2005). To test each model, 25% of the data in each run were randomly selected by Maxent and compared with the model output created with the remaining 75% of the presence data. We used threshold-independent receiver operating characteristic (ROC) analysis to evaluate the models (Phillips et al., 2006). The area under the ROC curve (AUC) provides a single measure of model performance, independent of choice of

threshold (Elith et al., 2006). An AUC of 0.5 indicates that the model fits occurrence data no better than random predictions, while a value of 1 indicates perfect fit of predictions with data.

1.3 Spatial analysis of species richness patterns

Because we were interested in richness patterns and processes at broad spatial scales, we rescaled the absence presence maps and environmental maps to 1° from their original resolutions using the software DIVA-GIS (version 5.2, <http://www.diva-gis.org>). Grid cells with less than 90% land cover were excluded from the analyses. Richness gradients for total bats and bat families were calculated by adding individual species' range maps.

We selected 10 climate, ambient energy and productivity variables that have been shown in previous studies to significantly relate to small mammal richness, particularly bat richness patterns (Andrews and O'Brien, 2000, Hawkins et al., 2003, Ruggiero and Kitzberger, 2004, Tognelli and Kelt, 2004, Thuiller et al., 2006, Levinsky et al., 2007, Whittaker et al., 2007, Qian et al., 2009). These include annual mean temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), seasonality of precipitation (BIO15), actual evapotranspiration (AET; Ahn and Tateishi, 1994), potential evapotranspiration (PET; Trabucco and Zomer, 2009) and Net Primary Product (NPP; Imhoff et al., 2004). Because of the inherent multicollinearity among the above variables, it is very difficult and indeed may be meaningless to distinguish among them (Hawkins et al., 2003, Field et al., 2009), and the statistical and inferential interpretation of their individual effects on the response variable (Graham, 2003). Thus, we reduced the dimensionality and removed the multicollinearity among these variables using a Principal Component Analysis (PCA; Graham, 2003), and from the resultant principal components interpreted new climate/ energy/ productivity variables.

We used elevation range (ERA), and number of ecoregions (NECO) as abiotic and biotic indicators of environmental heterogeneity, respectively. Using DIVA-GIS (version 5.2, <http://www.diva-gis.org>), ERA was calculated as the range of the altitude values (Farr et al., 2007) of the cells in a 3×3 neighbourhood around each cell (i.e. topographic heterogeneity), and NECO as the number of distinct classes of ecoregions (Olson et al., 2001) in a 3×3 neighbourhood around each cell (i.e. habitat heterogeneity).

To explore the congruence in species richness surfaces amongst the seven bat families, we used Pearson's correlations, and Clifford et al.'s (1989) method for estimating effective degrees of freedom to correct for spatial autocorrelation.

To examine the individual contribution of each explanatory variable to species richness patterns, we built non-spatial Ordinary Least Squares (OLS) regression models, and three spatial models (Bini et al., 2009): simultaneous autoregressive (SAR), conditional autoregressive (CAR), and eigen-vector-based spatial filtering (SEVM), using SAM software (Rangel et al., 2010). The degree of spatial autocorrelation in the standardised regression residuals was assessed using spatial correlograms of Moran's *I* coefficients calculated at 20 distance classes (Diniz-Filho et al., 2003). For the SEVM models, a truncation distance of 110 km, calculated in SAM, was used to create the spatial filters. Eigenvector filters with Moran's *I* coefficients in the first distance class >0.1 (Diniz-Filho and Bini, 2005), together with the environmental variables, formed the full model. We used an Akaike information criterion (AIC)-based approach to select the best OLS and SEVM models (Burnham and Anderson, 2002; Diniz-Filho et al., 2008). To compare the relative influence of the environmental drivers on the richness of total bat species and each family, we

performed multidimensional scaling (MDS, Primer version 5.2.2, PRIMER-E Ltd, 2001) on the Bray Curtis similarity matrix of the standardised coefficients of the model for each taxonomic group. MDS is a powerful tool to ordinate ecological data that do not follow standard statistical distributions by similarity indices or other measures of distance (Legendre and Legendre, 1998).

Violations to the assumption of stationarity, i.e. relationships among predictor and response variables are invariant throughout the entire span of the data, may lead to biases in estimated parameters of non-spatial and spatial curve-fitting models (Fotheringham et al., 2002). We used Geographically Weighted Regression (GWR) to test this assumption, and interpret geographically varying model parameters (da Silva Cassemiro et al., 2007). GWR was performed in SAM using a neighbourhood size of 10% of the dataset and a Gaussian distance weighting function.

To contrast the interpretation of the linear, curve-fitting models, we performed a Classification and Regression Tree (CART; De'ath and Fabricius, 2000) analysis using SPSS (version 19.0.0, IBM SPSS Statistics). This machine-learning method can capture non-stationary relationships, detect changes in relationships across space, and makes no assumptions about the shapes of dependent variable and predictor relationships (Hawkins, 2012). We performed an exhaustive search for univariate splits for each predictor variable at each node to find the split producing the greatest improvement in goodness of fit using the Gini measure of node impurity.

2 Results

2.1 Modelled species richness of bats

In total, 64 species from a total of 3,629 specimen occurrence records were modelled (Fig. 1); mean number of specimens per species = 56.6, ranging from 10 (e.g. *Chaerephon chapini*, *Cistugo seabrai*) to 301 (*Neoromicia capensis*). AUC values for Maxent analyses were > 0.9 for both training and test data. Temperature seasonality and precipitation of the wettest month contributed the most to Maxent development of potential distributions of bat species, and Jackknife analyses showed that temperature seasonality, particularly when used in isolation, contributed the most to model development for the majority of bat species.

Total bat species richness in southern Africa varied between 1 and 31 species (mean: 11 ± 8.87 SD; Fig. 2A). The main hotspot of bats was highest in the northeastern part of the region, in central Zimbabwe and along the border region with Mozambique. Additional hotspots were found along the eastern scarp of the Drakensburg Mountains, and in the southwestern Cape along the southern scarp of the Cape Fold Mountains. Richness patterns of bat families varied (Fig. 2B-i), ranging from Vespertilionidae being the most similar to total bat richness, to Miniopteridae being the least similar. Furthermore, the geographic distributions of richness patterns in bat families showed positive congruence between families ($r > 0.5$) except Pteropodidae and Miniopteridae (Table 1). Pteropodidae exhibited congruence only with Vespertilionidae, and Miniopteridae with Hipposideridae and Rhinolophidae. Emballonuridae was not compared with other taxonomic groups because species richness of this family was low ($n = 1$ species).

2.2 Environmental correlates of richness

The first four principal components explained 91.4% of the total variance of the environmental variables (eigenvalues 4.44–0.71; Table 2). All variables loaded high (> 0.7) and positively on PC1, except BIO3, BIO5, BIO15 and NPP. BIO5 loaded high on PC2, BIO3 loaded high on PC3 and BIO15 loaded high on PC4.

See Table 3 for the coefficients from the non-spatial and spatial models. ERA was positively correlated with richness, the primary predictor of total bat species richness and most family richness, and the only variable statistically significant in all OLS, CAR and SAR models. PC1 was also positively correlated with richness, and the primary predictor in Pteropodidae, Vespertilionidae and Nycteridae models. Non-spatial OLS models did not satisfy the assumption of independence of residuals: Moran's I in the first distance class of model residuals ranged between 0.502–0.702. Spatial autocorrelation in the residuals of the spatial models was removed (all Moran's $I < 0.05$) albeit to a different degree. SEVM models explained notably more of the variance in species richness (range of adjusted R^2 : 69%–84%) than OLS, CAR and SAR models (range of adjusted R^2 : 21%–51%). The combinations and ranks of coefficients of the OLS model were similar to those of the SAR model and to a lesser degree the CAR model, but typically differed from those of the SEVM model.

The combinations and ranks of coefficients also differed at family level. MDS grouped families based on coefficients to varying degrees from total bat species richness (Fig. 3A–D). The models for Vespertilionidae were the most similar to the models for total bat species richness, whilst those for Pteropodidae, Miniopteridae and Molossidae were the least similar.

There was a significant improvement in the GWR compared to the OLS model ($R^2 = 0.78$ and $= 0.42$, respectively; $F = 32.9$; $P < 0.001$; Fig. 4). Similar results were obtained for the bat families (Table 4). Thus, a highly significant non-stationarity was detected in the data set. The explanatory power (r^2) of the local regression is notably high in the south but low in the west of the region (Fig. 4C). Residuals of the GWRs contained minimal spatial autocorrelation (Moran's I at the first distance class equal to 0.05 [Pteropodidae] – 0.21 [Rhinolophidae]).

The CART analysis corroborated results from OLS, SAR and CAR analyses. The only explanatory variables that appeared in the regression tree were PC1 and ERA (Fig. 5). The first split was based on PC1, with values ≤ -0.876 in the left branch (explaining 35.9% of the total sum of squares), and values > -0.876 in the right branch (explaining 64.1% of the total sum of squares). Both nodes were subsequently split based on ERA; in node 1 with values ≤ 551.5 in the left branch (explaining 19.8 % of the total sum of squares) and > 551.5 in the right branch (explaining 16.2% of the total sum of squares) and in node 2 with values ≤ 458.0 in the left branch (explaining 39.5% of the total sum of squares) and > 458 in the right branch (explaining 24.6% of the total sum of squares). The normalised importance of ERA was 100% and that of PC1 was 82.1%.

3 Discussion

We found support for the predictions of both the habitat heterogeneity and climate hypotheses, and as expected, support varied among families and model selection. Non-spatial and spatial models revealed that both habitat heterogeneity, represented by altitude range (ERA), and climate, represented by PC1, were important predictors of species richness. However, ERA had the highest overall primacy in terms of explaining variance in bat species richness, and was the only significant environmental variable present in all models. Our results therefore caution the widely held opinion (Field et al. 2009) that species richness at broad spatial scales is most strongly influenced by climate and productivity whilst spatial heterogeneity plays a minor role.

The spatial richness patterns derived from the niche models were consistent with richness patterns of mammals, birds, and plants collated from a variety of available sources across southern Africa (Andrews and O'Brien, 2000; Jetz and Rahbek, 2002; Qian et al., 2009; Fig. 2A). Our strict selection criteria for the specimen data used in the niche-based

models means that our estimates of bat richness are relatively conservative but accurate. In support, estimates of richness from *in situ* sampling at 11 local sites across southern Africa compare well with our predicted species richness for the area (Table 5).

The principal components analysis of the environmental variables may be difficult to interpret and may be less correlated with bat species richness because each principal component is a linear combination of all the original variables. Nonetheless, we interpreted PC1 to be a proxy for climate acting directly through physiological effects, or indirectly through resource productivity or biomass, and found that it was positively correlated with bat richness in many non-spatial and spatial model curve fitting models, particularly in the models for Pteropodidae, Vespertilionidae and Nycteridae, as well as in the regression trees. In areas where PC1 and species richness is highest, the amount and duration of food resources is probably greatest, and here plant diversity is also greatest (Andrews and O'Brien, 2000; Qian et al., 2009). This is consistent with the region being characterised by a strong seasonal summer rainfall climate where the duration of the dry season ranges from < 1 month to > 7 months. The timing of parturition of African insectivorous bats is constrained by rainfall, because insect abundance peaks approximately a month after the rainfall season starts (Cumming and Bernard, 1997). Similarly, species richness of bats that eat nectar and fruit is high in areas of high rainfall and high plant diversity (Patten, 2004), and pteropodids such as *Epomophorus wahlbergi* time the birth of their pups to ensure concurrence between the post-weaning period and peak abundance of preferred fruit (Cumming and Bernard, 1997).

The standardised coefficients of the explanatory variables that comprised the non-spatial and spatial models differed among bat families, and clearly separated the Pteropodidae and Miniopteridae (except the SEVM model) from the other families (Fig. 3). In addition, the geographic distributions of richness patterns in these two bat families did not show positive congruence between most of the other families. Patten (2004) and Stevens (2004) also found differences in pattern and process of richness in New World bat families, but Ulrich et al. (2007) did not in European bat families, perhaps because their dataset included only one species from Pteropodidae (*Rousettus aegyptiaca*) and Miniopteridae (*Miniopterus schreibersii*). Most extant bat families appear to have evolved before the late Eocene, with the estimated divergence between Pteropodidae and the other Pteropodiformes families ca 52–65 MYA, and between Miniopteridae and Vespertilionidae ca 39–53 MYA (Eick et al., 2005). Fruits which are likely to be eaten by Pteropodidae are present in southern Africa throughout the year, whilst insect availability is highly seasonal (Cumming and Bernard, 1997). Roost availability probably limits the distribution of species that are obligate cave roosters such as miniopterids (Monadjem et al., 2010a). Thus, the differences in the species richness patterns, and type and rank of explanatory variables comprising the spatial and non-spatial models, probably reflect the interplay between the different ecologies and biogeographic history of bat families, mediated by significant climatic and geological changes across Africa since the Eocene.

Notwithstanding the causality issues that plague multiple regression models (Graham, 2003), there were differences in the composition of explanatory variables between spatial and non-spatial models, and the spatial models varied in the extent to which they minimized spatial autocorrelation. Similar to previous studies (Dormann et al., 2007; Kissling and Carl, 2008; Bini et al., 2009; Beale et al., 2010), the standardised coefficients of SEVM models (in which new spatial variables were added to the regression) differed more from the non-spatial, OLS model than those of SAR and CAR models (which modelled spatial autocorrelation in the residuals). Moreover, GWR indicated that the basic assumption of stationarity was violated. Because the data are non-stationary, single, semi-local regression coefficients generated by the spatial regressions cannot be interpreted with confidence because a unique local coefficient does not exist in the data

(Fotheringham et al., 2002). The GWR showed that the explanatory power of the local regression was high in the southern but low in the western regions. Compared with the rest of the region, little is known about the bat diversity in the west, which is reflected in the low number of museum specimens (Monadjem et al., 2010a). However, results from the CART analysis, which can capture non-stationary relationships, corroborated the strong association between richness and ERA and PC1. This suggests that there may be consistent macroecological interpretations of bat richness patterns in the region.

It may be easier to interpret the explanatory variables of richness by partitioning richness patterns into sets of species according to traits such as range size (Ruggiero and Kitzberger, 2004; Rahbek et al., 2007; Terribile et al., 2009). We did not deconstruct richness patterns into range size sets because the ranges of many species extend further north on the African continent. Furthermore, there is increasing evidence of a number of range-restricted cryptic species in the region yet to be or newly described (Monadjem et al., 2010b; Stoffberg et al., 2012; Taylor et al., 2012). There are also strong arguments in the literature for the influence of historical contingency, including the effects of colonization limitation, on species richness (Mittlebach et al., 2007). Additional study using a dated phylogeny of African bats, ideally allied with sufficiently detailed chronicles of palaeoenvironmental evolution, could reveal the rates and extend to which diversification influenced distribution patterns. This line of attack may be the most feasible route to evaluate ultimate causes of current richness patterns, which reflect on how the tempo and mode of evolutionary events interfaced with those that sculpted palaeo-environments.

To conclude, we found that both habitat heterogeneity and climate are, at least, proximate determinants of bat richness in southern Africa. Importantly, rank and composition of explanatory variables can be highly dependent on model selection and taxonomy, and should therefore be considered in future work. Now that the expected richness gradients are well defined, detailed ecological work on bat diversity can commence in zones with high spatial heterogeneity that are poorly sampled, and in richness hotspots that are impacted by human land use (Chown, 2010).

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Table 1 Congruence between bat families corrected for spatial autocorrelation using Clifford et al. (1989) method (Pearson's r above the diagonal, corrected P -values below the diagonal)

	Pteropodidae	Hipposideridae	Rhinolophidae	Nycteridae	Molossidae	Miniopteridae	Vespertilionidae
Pteropodidae	-	0.398	0.228	0.499	0.236	0.361	0.625
Hipposideridae	0.045	-	0.784	0.513	0.547	0.512	0.668
Rhinolophidae	0.196	<0.001	-	0.487	0.532	0.615	0.592
Nycteridae	0.076	0.016	0.013	-	0.647	0.243	0.691
Molossidae	0.274	0.008	0.009	0.004	-	0.265	0.707
Miniopteridae	0.091	0.003	<0.001	0.243	0.204	-	0.574
Vespertilionidae	0.02	<0.001	0.002	0.009	0.001	0.006	-

Table 2 Contribution of the first four principal components (PC1 – PC4) derived from principal components analysis of nine environmental variables (values in boldface indicate variables contributing most to the components)

Variable [†]	PC1	PC2	PC3	PC4
Bio1	0.877	-0.451	0.035	-0.069
Bio3	0.599	0.172	0.706	0.139
Bio5	0.380	-0.783	-0.355	-0.058
Bio6	0.884	-0.017	0.292	-0.139
Bio12	0.757	0.552	-0.229	0.065
Bio15	0.529	-0.409	-0.091	0.719
AET	0.760	0.509	-0.214	-0.095
PET	0.791	-0.435	-0.024	-0.355
NPP	0.574	0.629	-0.303	0.079
Eigenvalue	4.440	2.160	0.910	0.710

[†]Bio1 – annual mean temperature; Bio3 – isothermality; Bio5 – maximum temperature of the warmest month; Bio6 – maximum temperature of the coldest month; Bio12 – annual mean precipitation; Bio15 – precipitation seasonality; AET – actual evapotranspiration; PET – potential evapotranspiration; NPP – net primary productivity. We interpreted these variables as follows. PC1 describes the influence of climate, acting directly through physiological effects, or indirectly through resource productivity or biomass. PC3 and PC4 are measures of climate stability.

Table 3 Standardised coefficients of environmental correlates of richness for total bat species (Tbs) and seven families (Pte – Pteropodidae; Hip – Hipposideridae; Rhi – Rhinolophidae; Nyc – Nycteridae; Mol – Molossidae; Min – Miniopteridae; Ves – Vespertilionidae) estimated by non-spatial (OLS) and spatial (CAR, SAR, and SEVM) models

	Predictor ‡	OLS			CAR			SAR			SEVM†		
		AV	MAM	t	AV	t	prob	AV	t	prob	AV	MAM	t
Tbs	PC1	0.462	0.459	12.3	0.434	9.7	<0.001	0.44	8.9	<0.001	0.181	0.182	3.5
	PC2	-0.035			-0.013	0.3	0.743	0.104	2.4	0.019	0.283	0.281	6.6
	PC3	-0.226	-0.224	5.9	-0.191	4.7	<0.001	-0.068	1.6	0.115	-0.122	-0.123	3.7
	PC4	-0.049			-0.014	0.4	0.714	-0.07	1.8	0.078	-0.12	-0.12	3.3
	ERA	0.507	0.501	12.4	0.492	10.6	<0.001	0.429	9.8	<0.001	0.109	0.109	2.8
	NECO	0.201	0.204	5.6	0.177	5.0	<0.001	0.134	3.9	<0.001	-0.032		
	AIC	3109.1	3107.7		3069.7			3111.5			2446.7	2534.2	
	Moran's <i>I</i>	0.74	0.70		0.24			0.18			0.03	0.03	
	<i>R</i> ²	0.42	0.41		0.46			0.42			0.84	0.84	
Pte	PC1	0.65	0.659	18.9	0.594	14.9	<0.001	0.491	9.8	<0.001	0.762	0.759	13.8
	PC2	0.211	0.208	5.7	0.245	6.8	<0.001	0.183	4.4	<0.001	0.59	0.595	12.0
	PC3	-0.186	-0.188	5.3	-0.18	4.9	<0.001	-0.232	5.6	<0.001	-0.067	-0.067	1.8
	PC4	-0.112	-0.113	3.6	-0.076	2.3	0.024	0.007	0.2	0.861	0.031		
	ERA	0.327	0.334	7.9	0.289	7.0	<0.001	0.185	4.4	<0.001	-0.012		
	NECO	-0.068	-0.068		-0.055	1.7	0.087	-0.042	1.3	0.202	-0.089	-0.09	2.1
	AIC	1487.4	1487.3		1540.8			1461.6			1091.7	1174.2	
	Moran's <i>I</i>	0.57	0.58		0.15			0.13			0.04	0.04	
	<i>R</i> ²	0.51	0.51		0.46			0.54			0.78	0.78	
Hip	PC1	0.301	0.297	6.7	0.262	4.9	<0.001	0.293	4.6	<0.001	0.053		
	PC2	-0.162	-0.159	3.5	-0.145	3.0	0.003	-0.002	0.04	0.965	0.171	0.171	3.1
	PC3	-0.252	-0.249	5.6	-0.205	4.2	<0.001	-0.094	1.8	0.075	-0.275	-0.272	6.1
	PC4	0.138	0.139	3.5	0.151	3.4	<0.001	0.073	1.5	0.128	0.082	0.076	1.7
	ERA	0.461	0.455	8.5	0.436	7.9	<0.001	0.404	7.6	<0.001	0.17	0.159	3.1
	NECO	0.099	0.098	2.3	0.083	1.9	0.053	0.04	1.0	0.33	-0.04		
	AIC	1109.3	1109.2		1067.9			1070.7			598.6	681.5	

	Moran's <i>I</i>	0.56	0.58		0.16			0.1			0.002	0.002	
	<i>R</i> ²	0.21	0.21		0.28			0.28			0.72	0.72	
Rhi	PC1	0.074	0.077	1.8	0.056	1.0	0.29	0.11	1.8	0.074	-0.139	-0.146	2.5
	PC2	-0.183	-0.193	4.2	-0.175	3.7	<0.001	-0.003	0.05	0.957	0.142	0.13	2.8
	PC3	-0.098	-0.103	2.3	-0.066	1.4	0.172	0.096	1.9	0.06	-0.099	-0.109	3.0
	PC4	0.071	0.071	1.8	0.11	2.5	0.013	0.006	0.1	0.9	-0.068	-0.075	1.9
	ERA	0.456	0.481	9.0	0.476	8.7	<0.001	0.419	8.2	<0.001	0.076	0.079	1.9
	NECO	0.2	0.191	4.5	0.159	3.8	<0.001	0.116	2.9	0.004	0.058		
	AIC	1747.3	1747.1		1726.2			1709.6			1037.1	1119.7	
	Moran's <i>I</i>	0.65	0.63		0.2			0.15			0.02	0.02	
	<i>R</i> ²	0.23	0.23		0.26			0.29			0.81	0.81	
Nyc	PC1	0.607	0.6	16.7	0.587	13.7	<0.001	0.516	9.8	<0.001	0.048		
	PC2	-0.296	-0.292	7.8	-0.293	7.6	<0.001	-0.252	5.7	<0.001	-0.308	-0.311	6.8
	PC3	-0.452	-0.449	12.1	-0.421	10.7	<0.001	-0.326	7.5	<0.001	-0.174	-0.173	4.8
	PC4	-0.027			<0.001	<0.001	1	-0.039	1.0	0.333	-0.334	-0.338	9.4
	ERA	0.57	0.561	12.8	0.551	12.4	<0.001	0.469	10.6	<0.001	0.203	0.201	4.8
	NECO	0.049	0.05	1.4	0.027	0.8	0.426	0.018	0.5	0.6	-0.119	-0.118	3.0
	AIC	1039.1	1028.6		1046.9			1107			522.8	608.7	
	Moran's <i>I</i>	0.67	0.63		0.2			0.21			0.03	0.03	
	<i>R</i> ²	0.48	0.48		0.46			0.39			0.81	0.81	
Mol	PC1	0.213	0.213	5.5	0.234	5	<0.001	0.246	4.3	<0.001	-0.184	-0.184	3.2
	PC2	-0.234	-0.234	5.8	-0.254	6.0	<0.001	-0.131	2.8	<0.001	-0.192	-0.193	4.1
	PC3	-0.444	-0.444	11.2	-0.419	9.8	<0.001	-0.26	5.5	<0.001	-0.182	-0.182	5.0
	PC4	0.193	0.193	5.5	0.2	5.1	<0.001	0.096	2.7	0.006	-0.124	-0.125	3.2
	ERA	0.325	0.325	6.8	0.329	6.8	<0.001	0.305	6.5	<0.001	0.131	0.132	3.1
	NECO	0.318	0.318	8.4	0.299	8.0	<0.001	0.248	6.7	<0.001	0.003		
	AIC	1590.1	1590.1		1557.6			1603.2			993.5	1081.1	
	Moran's <i>I</i>	0.69	0.66		0.14			0.14			0.02	0.01	
	<i>R</i> ²	0.39	0.39		0.43			0.37			0.81	0.81	
Min	PC1	0.119	0.115	2.8	0.115	2.4	0.08	0.274	4.8	<0.001	0.136	0.136	1.8
	PC2	0.162	0.167	4.0	0.177	4.1	<0.001	0.368	7.6	<0.001	0.421	0.431	7.2

	PC3	-0.051			-0.023	0.5	0.609	0.143	3.0	0.003	-0.102	-0.106	2.3
	PC4	-0.217	-0.217	5.8	-0.187	4.6	<0.001	-0.278	6.4	<0.001	-0.16	-0.147	2.9
	ERA	0.403	0.391	8.8	0.413	8.3	<0.001	0.411	8.6	<0.001	0.181	0.197	3.6
	NECO	0.121	0.123	3.1	0.092	2.4	0.018	0.048	1.3	0.2	-0.001		
	AIC	814.5	813.7		833.9			749			426.8	510.5	
	Moran's <i>I</i>	0.49	0.50		0.12			0.012			0.03	0.03	
	<i>R</i> ²	0.31	0.31		0.29			0.4			0.69	0.69	
Ves	PC1	0.505	0.506	14.2	0.493	11.5	<0.001	0.478	9.3	<0.001	0.05		
	PC2	0.017			0.025	0.6	0.526	0.127	2.9	0.004	0.203	0.194	4.4
	PC3	-0.299	-0.3	8.3	-0.258	6.6	<0.001	-0.147	3.5	<0.000	-0.138	-0.142	4.1
	PC4	-0.123	-0.123	3.7	-0.104	2.9	0.004	-0.156	4.0	<0.001	-0.257	-0.265	7.6
	ERA	0.442	0.444	11.5	0.411	9.2	<0.001	0.364	8.5	<0.001	0.087	0.084	2.1
	NECO	0.216	0.215	6.1	0.199	5.8	<0.001	0.158	4.7	<0.001	-0.052		
	AIC	2421.9	2419.9		2382.1			2427.8			1861.8	1947.2	
	Moran's <i>I</i>	0.71	0.68		0.18			0.14			0.03	0.03	
	<i>R</i> ²	0.46	0.46		0.51			0.46			0.83	0.83	

[†] SEVM models composed of environmental correlates and 41 eigenvector filters

[‡] PC1 – PC4 are the first four principal components derived from a principal components analysis of nine environmental variables (Table 2), ERA is altitude range, and NECO is the number of ecoregions.

Coefficients are shown for the average model weighted by w_i (AV), and the minimum adequate model (MAM; i.e. the model with $\Delta AIC_i = 0$) for the OLS and SEVM models. Also given are the *t*-values (bold shows highest value, i.e. the primary predictor), probability for CAR and SAR models, Moran's *I* residual autocorrelation, the value of the Akaike Information Criterion (AIC), and *R*² of the AV and MAM models.

Table 4 Model parameter estimates from geographically weighted regression for total bat species and seven families. The median and inter-quartile range in local parameter estimates is shown.

Predictor [†]	Total bat species			Pteropodidae			Hipposideridae			Rhinolophidae		
	Median	25%	75%	Median	25%	75%	Median	25%	75%	Median	25%	75%
PC1	0.761	0.193	2.296	0.329	0.06	0.521	0.088	-0.081	0.207	0.022	-0.106	0.265
PC2	0.246	-0.352	1	0.356	0.271	0.454	-0.05	-0.097	0.026	-0.137	-0.264	0.0168
PC3	-0.299	-1.821	0.287	-0.292	-0.435	-0.226	-0.019	-0.063	0.053	0.134	0.044	0.393
PC4	-0.069	-0.644	0.485	-0.089	-0.31	0.188	0.0008	-0.046	0.145	0.205	-0.047	0.355
ERA	0.009	0.004	0.014	0.001	0.0002	0.002	0.001	0.0003	0.0016	0.002	0.0006	0.003
NECO	0.368	0.142	0.605	0.009	-0.02	0.026	0.015	-0.003	0.041	0.051	-0.0007	0.104
Moran's <i>I</i>	0.16			0.05			0.13			0.21		
<i>R</i> ²	0.78			0.77			0.63			0.7		

Predictor [†]	Nycteridae			Molossidae			Miniopteridae			Vespertilionidae		
	Median	25%	75%	Median	25%	75%	Median	25%	75%	Median	25%	75%
PC1	0.231	0.169	0.333	0.298	0.158	0.399	-0.013	-0.138	0.165	0.627	0.209	1.284
PC2	-0.141	-0.449	0.018	-0.447	-0.654	0.071	0.153	0.07	0.19	0.038	-0.245	0.672
PC3	-0.406	-0.626	-0.092	-0.597	-0.974	-0.137	0.025	-0.037	0.224	-0.817	-1.554	0.027
PC4	0.126	-0.009	0.27	0.332	0.105	0.518	-0.081	-0.25	-0.035	-0.376	-0.73	-0.038
ERA	0.001	0.0003	0.002	0.001	0.0003	0.002	0.0007	0.0003	0.001	0.004	0.002	0.006
NECO	-0.002	-0.038	0.018	0.121	0.091	0.174	0.003	-0.011	0.015	0.209	0.076	0.325
Moran's <i>I</i>	0.08			0.12			0.06			0.15		
<i>R</i> ²	0.78			0.72			0.74			0.78		

[†] PC1 – PC4 are the first four principal components derived from a principal components analysis of nine environmental variables (Table 2), ERA is altitude range, and NECO is the number of ecoregions.

Table 5 Estimates of bat richness at 1° versus *in situ* sampling at a local scale

Site	GPS	Richness map	In situ estimate	Source [†]
AFH	32°22' S, 19°03' E	10	11	¹
De Hel	33°05' S, 19°05' E	10	7	¹
De Hoop	34°26' S, 20°25' E	9	7	¹
Durban	29°50' S, 30°56' E	27	23	^{2,3,4}
Goodhouse	28°56' S, 18°07' E	7	9	¹
Hlane- Mlawula-Mbuluzi	26°22' S, 32°10' E	21	20	⁵
Knysna	33°57' S, 23°10' E	6	7	¹
Kwalata	25°23' S, 28° 19' E	6	7	¹⁰
Mkuze	27°24' S, 32°39' E	21	21	^{7,8,9}
Pafuri	22°43' S, 31°19' E	23	26	⁶
Sudwala	25°22' S, 30°42' E	19	18	¹

Source: ¹Schoeman & Jacobs, 2011, ²Schoeman & Waddington, 2011 and references therein, ³Durban Natural Science Museum, unpublished data,

⁴Moonsamy, 2012*, ⁵Monadjem & Reside, 2008, ⁶Aldridge & Rautenbach, 1987, ⁷M.C. Schoeman, P.J. Taylor, & G. Delcros, unpublished data,

⁸Taylor et al., 2007, ⁹D'Cuze et al., 2008, ¹⁰Pierce, 2012[&].

* Moonsamy S, 2012. The relative influence of local and landscape processes on the structure of insectivorous bat ensembles in urban nature reserves. Unpublished MSc thesis. University of KwaZulu Natal, Durban.

& Pierce MW, 2012. Assessing bat (Chiroptera) diversity: Determinants of assemblage and ensemble structure at Kwalata Game Ranch, Gauteng, South Africa. Unpublished MSc thesis. University of Witwatersrand, Johannesburg.

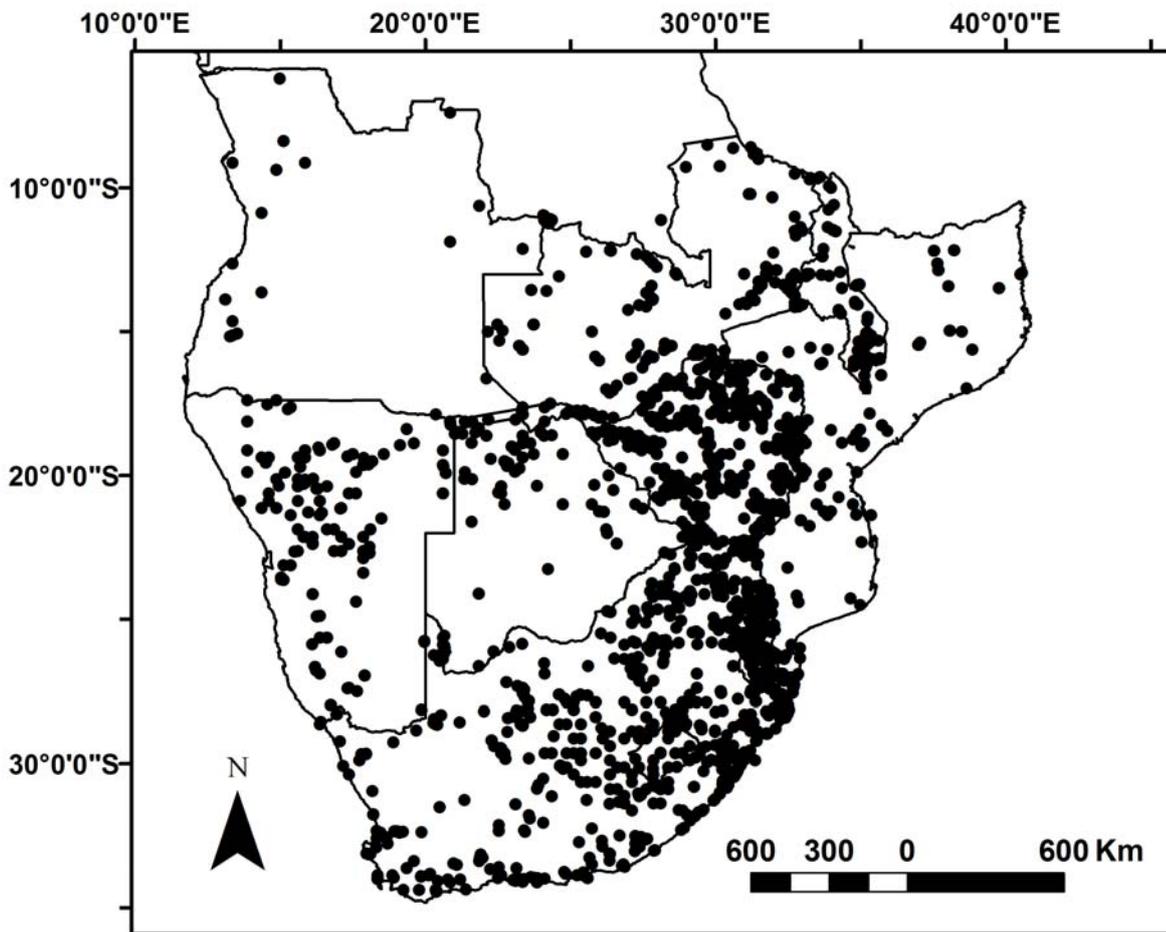


Fig. 1 Map showing distribution of the 3629 museum specimen records used to model the distribution ranges of species

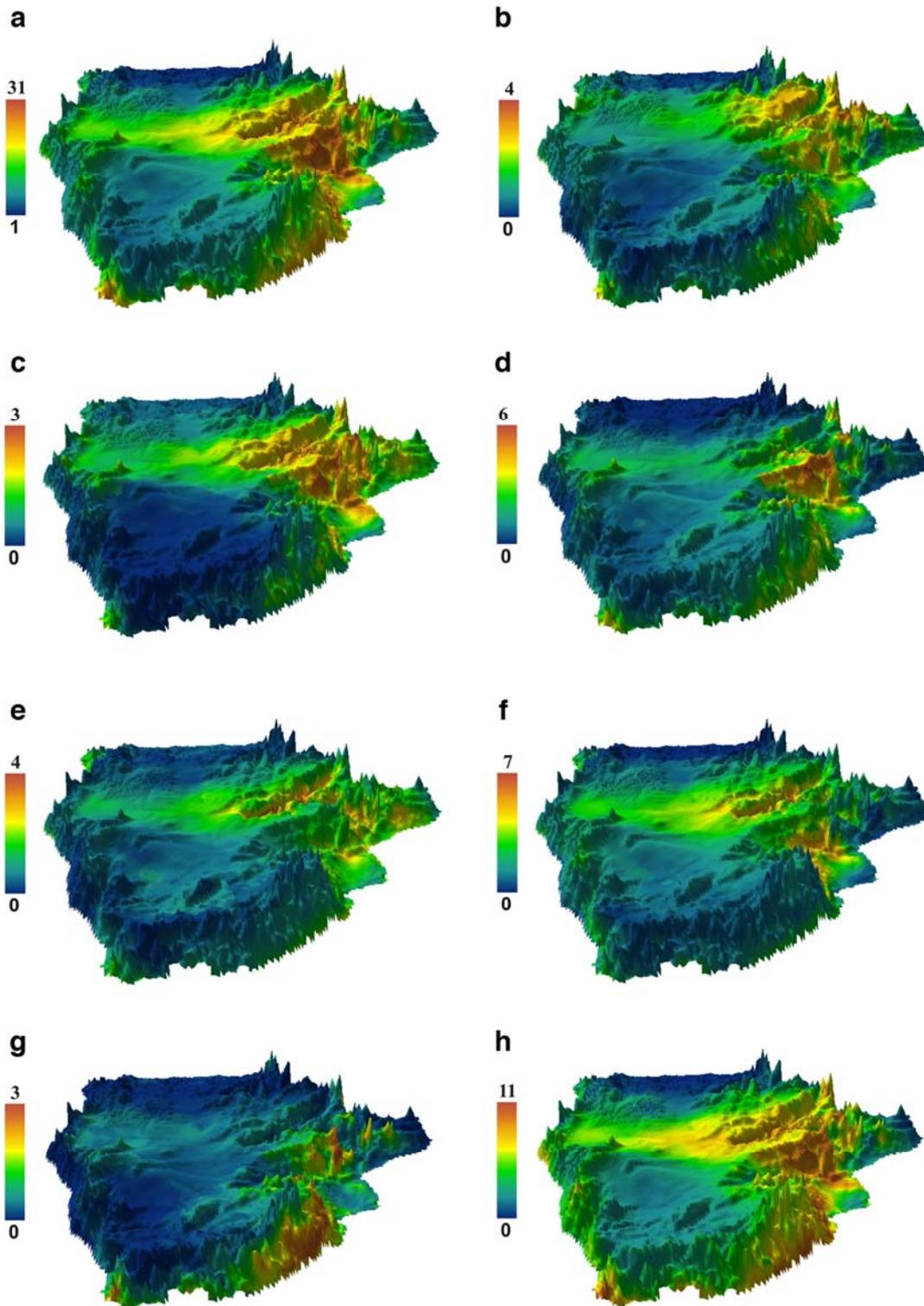


Fig. 2 Geographic distribution of richness in Total bat species (A), Pteropodidae (B), Hipposideridae (C), Rhinolophidae (D), Nycteridae(E), Molossidae (F), Miniopteridae(G), and Vespertilionidae (H) draped over a topographical surface at 2.5 minute resolution

Vertical extrusion is linear with elevation.

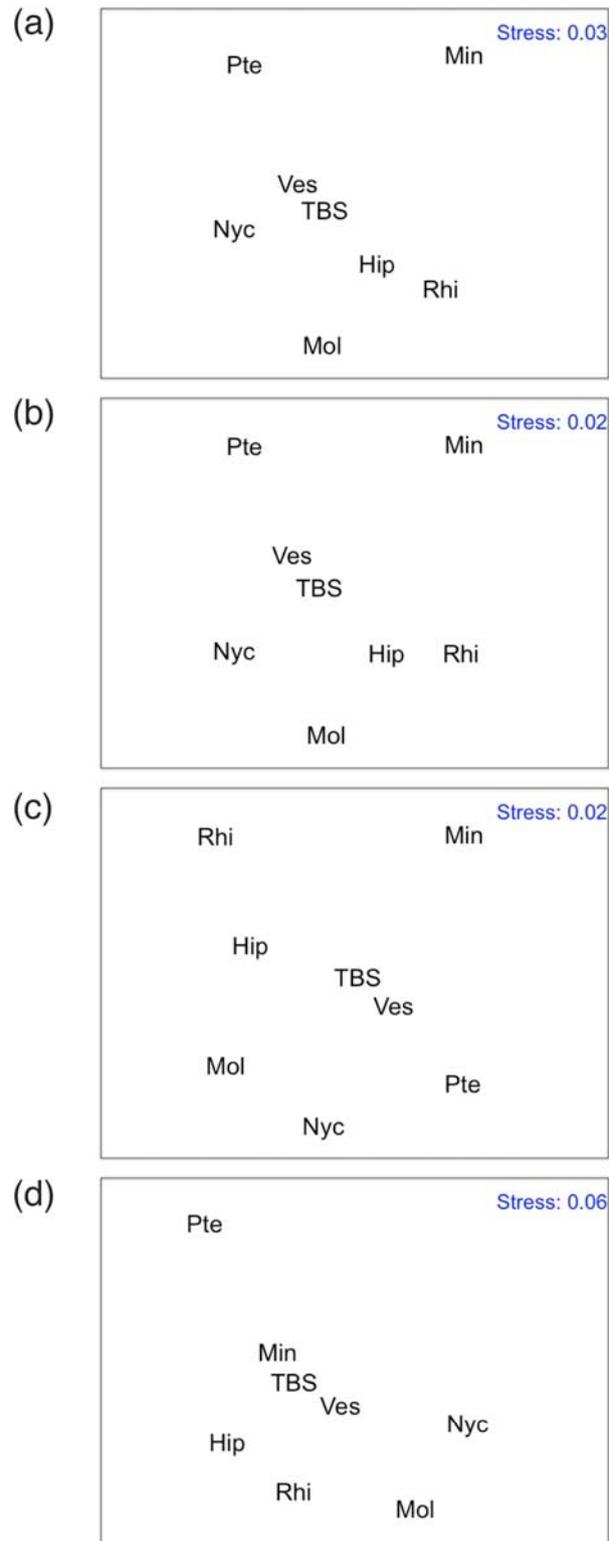


Fig. 3 MDS-plots of standardised coefficients of the explanatory variables that comprised non-spatial OLS (A) and spatial SAR (B), CAR (C) and SEVM (D) models for total bat species (TBS) and seven families

Pte – Pteropodidae; Hip – Hipposideridae; Rhi – Rhinolophidae; Nyc – Nycteridae; Mol – Molossidae; Min – Miniopteridae; Ves – Vespertilionidae. Small stress values (< 0.1) of the MDS-plots indicate that the goodness-of-fit of the reproduced distance matrices to the observed distance matrices are satisfactory (Kruskal and Wish, 1978).

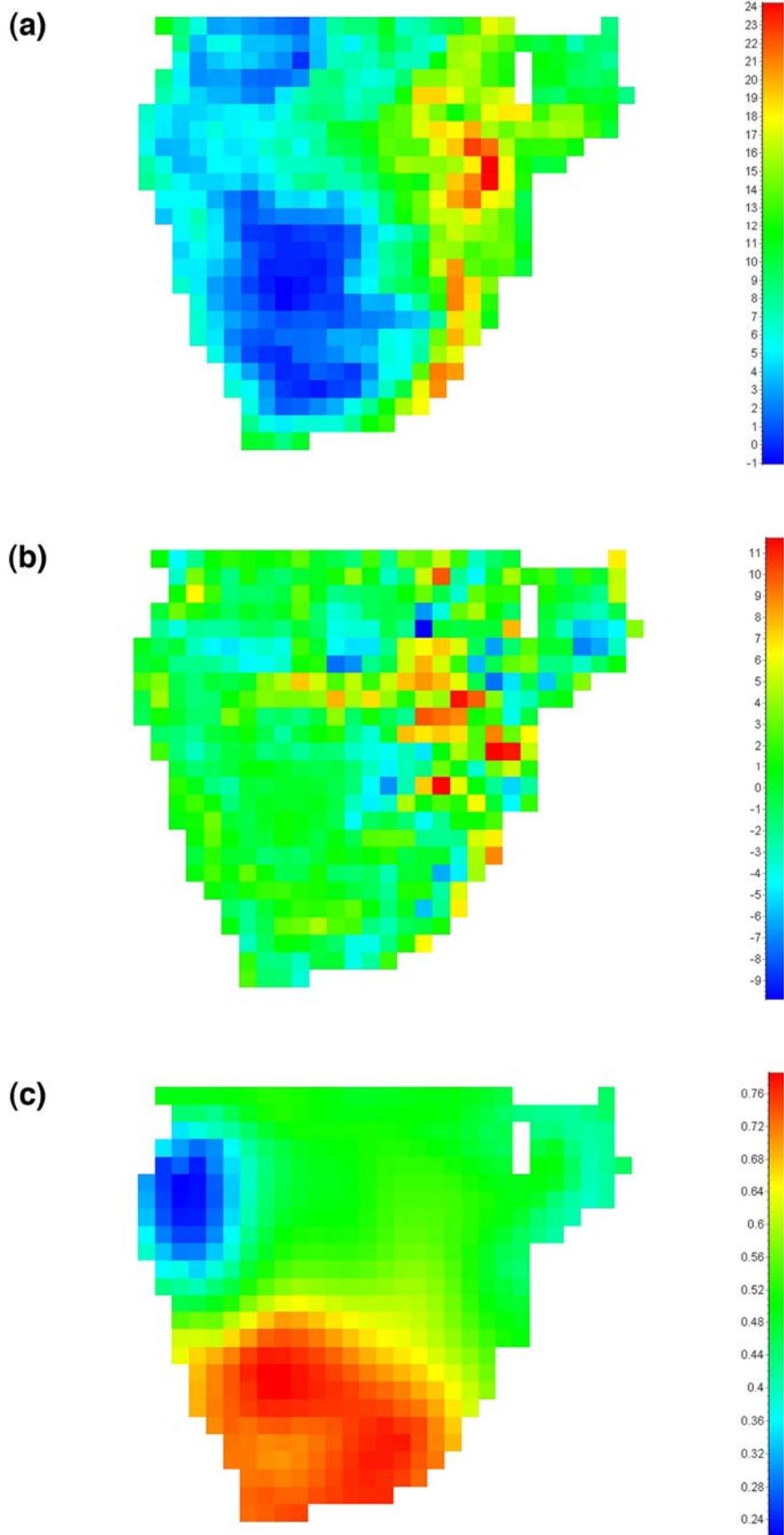


Fig. 4 Patterns of spatial variation in regression parameters from geographically weighted regression, including estimated species richness (A), residuals (B) and the model fit, given by r^2 (C)

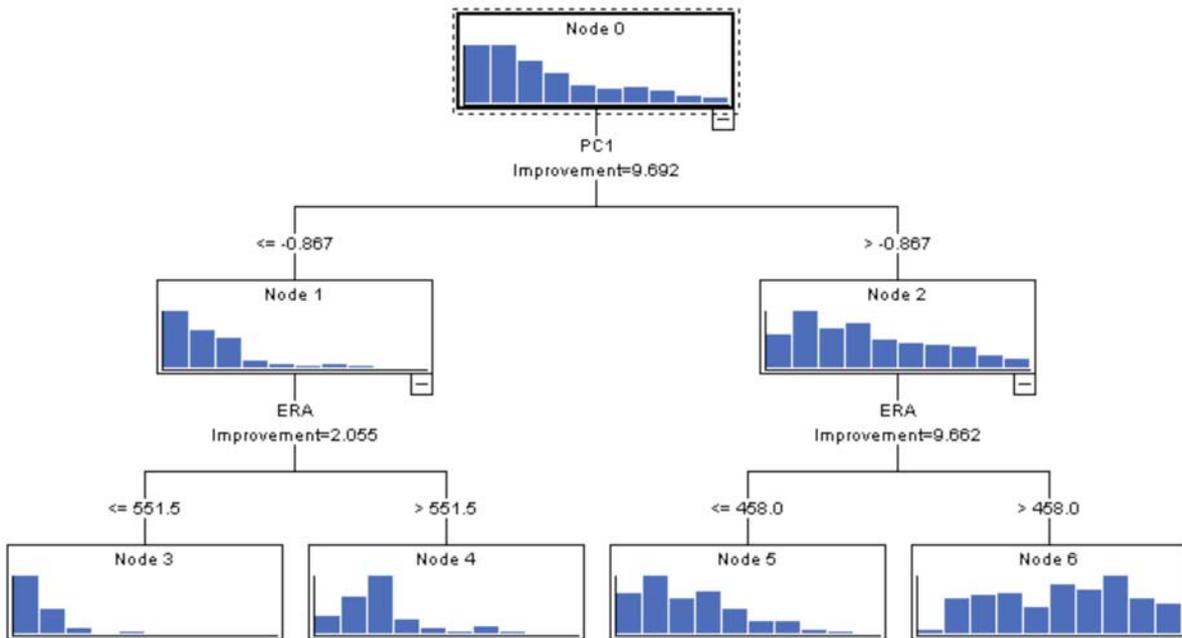


Fig. 5 CART analysis of total bat species richness in southern Africa

The significant explanatory values were ERA (altitude range) and PC1 (climate/productivity/energy variable derived from PCA; see Table 2). Each of the splits (nonterminal nodes) is labelled with the variable and its values that determine the split. For each of the nodes, the distribution of the observed values of bat species richness is shown in a histogram.