

Predictors of mammal species richness in KwaZulu-Natal, South Africa



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ABSTRACT

The management of multi-functional landscapes warrants better knowledge of environment-richness associations at varying disturbance levels and habitat gradients. Intensive land-use patterns for agricultural purposes lead to fragmentation of natural habitat resulting in biodiversity loss that can be measured using landscape metrics to assess mammalian richness. Since carnivores and herbivores are likely to show different responses to disturbance, we calculated carnivore, non-carnivore, and total mammal species richness from camera surveys using a first order Jackknife Estimator. Richness was compared along a habitat gradient comprising coastal forest, *Acacia* thicket, and highland in KwaZulu-Natal, South Africa. We used standardized OLS regression models to identify climatic and disturbance variables, and landscape metrics as predictors of species richness. The estimated total and non-carnivore species richness were highest in coastal forest, while carnivore species richness was highest in highland followed by coastal forest and *Acacia* thicket. Average monthly maximum temperature was a significant predictor of all richness groups, and precipitation of the wettest month and isothermality determined total and non-carnivore species richness, respectively. These climatic variables possibly limit species distribution because of physiological tolerance of the species. Total mammal richness was determined by mean shape (+) and habitat division (–) while diversity (+) and patch richness (–) explained carnivore species richness. Mean shape index (+) influenced non-carnivore richness. However, habitat division and patch richness negatively influenced total mammal richness. Though habitat patch size and contiguity had a weak positive prediction, these metrics demonstrated the importance of habitat connectivity for maintaining mammal richness. The identification of these climatic and landscape patterns is important to facilitate future landscape management for mammal conservation in forest-mosaics.

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1. Introduction

Mammalian richness is an effective indicator for prioritizing biodiversity conservation in environmental decision making and management. Species richness is usually driven by vegetation under the influence of local climatic variation, and may be affected by exposure to various levels of disturbance. Climate modulates the geographic distribution of individual species, which then interact to influence species richness. Temperature can limit species distribution depending on the physiological tolerances of taxa (Currie, 1991; O'Hara and Tittensor, 2010) and several studies show how climate largely shapes species richness (Field et al., 2009; Jetz et al., 2009; Davies et al., 2011). Further, water availability, vegetation productivity and landscape structure drive regional variation in richness at multiple levels (Currie, 1991; Olff et al., 2002; McGarigal et al., 2005; Yates et al., 2012; Del Toro, 2013). Increased habitat

loss and fragmentation has challenged biodiversity persistence in recent centuries because of reduction in habitat availability and increasing habitat isolation: i.e. small isolated patches constrain species to survive within small local populations (McGarigal and Marks, 1995; Fahrig, 2003; Fischer and Lindenmayer, 2007). However, at the landscape level, changes in species richness may be predicted along environmental gradients (McGarigal et al., 2005; Schindler et al., 2008) and habitat fragmentation and loss are considered as major determinants of biodiversity decline worldwide (Schindler et al., 2008; Hu et al., 2012). Intensive land uses for agricultural purposes lead to fragmented natural habitats resulting in smaller and more isolated patches (Hoffmann and Greif, 2003; Morelli, 2013; Ramesh et al., 2015), which in turn reduce habitat connectivity, inhibit animal movements and ecological processes (Kozakiewicz, 1993; Crooks et al., 2011). Forest specialists dependent on remnant forest patches in agricultural landscapes suffer from deleterious effects through altered biotic and abiotic processes associated with reduced patch size, increased length of forest edges, and patch isolation (Woodroffe and Ginsberg, 1998). Species survival depends on the amount of space between patchily

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Table 1

Camera trap surveys carried out in three study regions of KwaZulu-Natal, South Africa.

Study area	Central coordinate	Average annual minimum and maximum temperature (°C)	Annual rainfall (mm)
Fort Nottingham	E 29°57'21.6", S 29°25'30.0"	9.2; 20.08	975
Ashburton	E 30°26'20.4", S 29°41'38.4"	13; 23.50	620–720
False Bay Park	E 32°21'38.7", S 27°58'13.4"	15.5; 28.0	950

distributed habitats in a fragmented landscape, and change in habitat structure accelerates species extinction (Morelli, 2013). Therefore, assessments of the effects of landscape structure on mammalian richness is an important step for wildlife conservation and landscape restoration planning that may help to determine distributional patterns of mammals and their responses to habitat fragmentation and loss. In this context, effective conservation warrants understanding the effects of landscape metrics such as habitat patch size, shape, connectivity and other patch characteristics on species richness, and how richness patterns are driven by bioclimate and landscape structure (McGarigal et al., 2005; Ewers and Didham, 2006) in protected and disturbed areas.

As land-use patterns change, we can monitor the way species distributions respond accordingly. The expansion of species distribution is limited to varied natural conditions and development in the landscape (Van der Putten et al., 2010). Therefore richness relationships can differ among biogeographic regions and global scale responses might not reflect responses at the regional level (Saunders et al., 1991; Kissling et al., 2009). The use of species richness models at smaller spatial scales is now benefiting local conservation actions. Other potential determinants of species richness include food availability, trophic interactions, predator pressure, hunting for bush meat and traditional medicine and expansion of invasive predators such as feral dogs and cats (Hawkins and Porter, 2003; Karanth et al., 2004; Kissling et al., 2007; Jetz et al., 2009; Greve et al., 2012; Kiffner et al., 2015).

Previous assessments on the distribution of mammalian biodiversity in South Africa relied on secondary sources such as range maps (Siegfried and Brown, 1992; Freitag and Van Jaarsveld, 1995) and museum specimen records (Gelderblom et al., 1995; Mugo et al., 2005; Rowe-Rowe and Taylor, 1996). Mammals are ideal indicators to study defaunation effects, and standardized camera trapping can be implemented easily and replicated at regional scales (Ramesh et al., 2015). Therefore, we used comprehensive camera surveys (or field surveys) to better understand species richness patterns across habitat gradients (Msuha et al., 2012; Ramesh et al., 2015). The estimation of true species richness in a community is important as observed richness is most likely an underestimate of true richness (Fleishman et al., 2006; Gotelli and Colwell, 2011). In this study we measured species richness using randomized species accumulation curves, a first-order of non-parametric Jackknife Estimator (Gotelli and Colwell, 2011; Colwell et al., 2012).

Using this, we aimed to determine the relative importance of environmental variables and landscape metrics in explaining mammal species richness (carnivore, non-carnivore and total species richness) using camera-trap surveys in three intensive study areas that represent three major habitats in KwaZulu-Natal, South Africa. Carnivores and herbivores identified in this study are two distinct mammal groups that are likely to show different responses to disturbances and environmental factors. Therefore, we tested the predictions that (1) mammal richness would vary along the habitat gradients, particularly with low mammal richness expected where habitat is prone to higher disturbance, and (2) carnivore and non-carnivore richness would increase with temperature and less fragmentation. We developed a series of regression models to test the predictions of mammal richness patterns and thereafter

used the model selection procedure to identify the relationships between predictor and richness.

2. Materials and methods

2.1. Study region

We sampled mammals across three sites spanning various altitude ranges and three habitat classifications within KwaZulu-Natal of South Africa: (1) highlands Sourveld grassland connected with patch of mist belt forest (>1200 m asl), (2) *Acacia* thickets (600–800 m asl), (3) coastal forest (<100 m asl; False Bay Park) (Mucina and Rutherford, 2006; Fig. 1). Both elevation and habitat influence the climate at each site (Table 1). The highland area is exposed to moderate levels of human disturbance while the *Acacia* thicket is subject to high anthropogenic disturbance based on land use patterns. Both of these habitats are heavily encroached for agricultural practices. The land uses include seed potato, plantation, livestock grazing and dairy production in indigenous grassland, pastures and maize (Ramesh et al., 2015). The coastal forest forms part of a protected area network, encompassing a part of Lake St. Lucia, a UNESCO World Heritage site. This protected area comprises sand forest, thornveld and open savanna. In coastal forest and *Acacia* thicket areas some ungulate species were introduced, which may inflate species richness; however, the potential effects of this are not considered in our study.

2.2. Data collection and analysis

We deployed infrared camera traps (Camera Ltl Acorn®6210MC, Shenzhen Ltl Acorn Electronics Co. Ltd., China), to “capture” photographs of mammalian species (1–2000 kg) in the study areas. We conducted camera trapping for 21 days at 42 camera sites located within three areas during January 2012 to April 2013. The average minimum inter-trap distance was 1.0 km to aid in spatial independence. The photographic delay between pictures was 30 s and the sensor sensitivity was set to high. Cameras were placed along animal trails and dirt roads at 20 cm above the ground and left to operate for 24 h every day. Vegetation was removed within the view range of cameras to avoid blank shots. Data were retrieved from cameras on a weekly basis. Photographic sequences were grouped into independent photographic events following Ramesh et al. (2012). The number of independent photographs was converted into presence/absence of mammalian species at each site per day.

Mammal distributions are generally determined by ecological requirements at their core area use (Samuel et al., 1985). Since vegetation in the three study areas is driven by local climatic variations, we expected differences in mammal distributions. The study regions are prone to fragmentation because of farming activities (Ramesh et al., 2015). Therefore, we used fragmentation metrics as predictors of mammal richness patterns. We incorporated possible predictive variables at every camera site including bioclimate, land-cover, vegetation indices, topography and anthropogenic disturbance (Table S1). Temperature has been frequently used as a proxy for climate change in relation to the environment; therefore, we used 19 ‘bioclimatic’ variables and other climatic variables

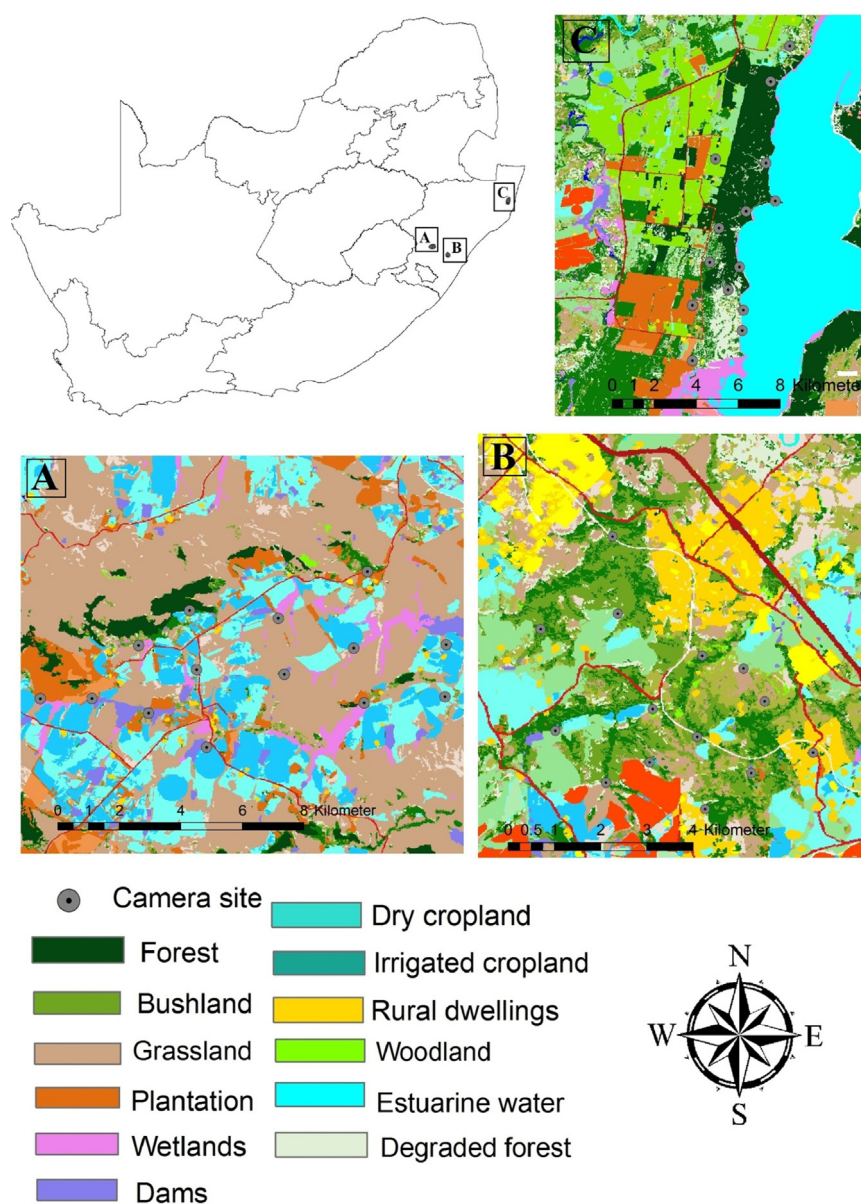


Fig. 1. Map of the three study sites with camera trap stations in KwaZulu-Natal, South Africa (A, highland; B, *Acacia* thicket, and C, coastal forest).

(average monthly mean, minimum and maximum temperature and monthly precipitation) from WORLDCLIM database (Hijmans et al., 2005). We extracted an elevation layer at 1 km² resolution from the Shuttle Radar Topography Mission (SRTM) elevation database (<http://srtm.csi.cgiar.org>). We used the Spatial Analyst tool in ArcGIS 9.3.1 (ESRI, Redlands, CA, USA) to calculate slope and aspect from the elevation layer. We extracted all remotely sensed layers using ArcGIS 9.3.1. Actual evapo-transpiration (AET, the amount of water removed from the soil through evaporation and transpiration). We extracted the mean AET values at 30 arc-seconds (mm) from <http://www.cgiar-csi.org> (Trabucco and Zomer, 2010) for each site. AET and precipitation variables are water budget factors providing information on the effective moisture regime (Hijmans et al., 2005). They are a proxy for net-primary productivity which is strongly related to woody plant species richness (Andrews and O'Brien, 2000). Therefore, these could be effective positive predictors of herbivore diversity. We downloaded the Human Influence Index as a measure of disturbance (HII; Last of the Wild Data Version 2, 2005) that may negatively affect species richness. Areas with high Monthly Normalized Difference Vegetation Index

(NDVI) support large herbivore numbers thereby enhancing carnivore species richness. We used NDVI from Advanced Very High Resolution Radiometer (AVHRR) sensor as a measure of vegetation production where a value of zero indicates no green vegetation and close to +1 (0.8–0.9) indicates the highest possible density of green leaves. We projected and re-sampled all environmental variables to a resolution of 1 km² using the Zonal Statistic tool in the Spatial Analyst toolbox in ArcGIS 9.3.1. Landscape metrics; mean patch area, shape index, richness, largest patch index, Shannon diversity, contiguity, division and mean radius of gyration etc. were calculated from the latest classified land-cover map 2008 of KwaZulu-Natal (Table S2; Geoterrimage, 2010; detailed descriptions of the matrices refer to McGarigal et al. (2002)). We used the land-cover map with a grain size of 20 m to compute landscape metrics in the program Fragstats 4.2 (McGarigal et al., 2002). Domestic carnivores can negatively impact the spatial distribution of native mammals. Therefore, we calculated the capture rate (number of independent photographs/trap nights) of feral dog *Canis lupus familiaris* and cat *Felis catus* from camera surveys and used these as possible influencing variables.

2.3. Data analysis

The incidence data (presence or absence) of each species in each sampling unit can be used to accurately record mammal species richness (Colwell, 2013). Therefore, it is possible to use 'sample-based incidence data' (Gotelli and Colwell, 2001). We estimated mammalian richness based on the presence-absence data using a first-order of nonparametric Jackknife Estimator in EstimateS (Version 9.0) (Colwell, 2013). Chi-square tests were used to compare observed and expected mammalian species richness. In addition, we used Mann-Whitney tests to compare mammalian species richness; total species richness, carnivore species richness and non-carnivore species richness among the three habitats in Program R (R Development Core Team, 2014).

The predictors' effect (independent variable) on patterns of mammalian richness (dependent variable) was assessed using a standard multiple ordinary least squares (OLS) regression. Spatial autocorrelation is often found in ecological studies which may lead to Type I error estimates from an inflation of degrees of freedom (Diniz-Filho et al., 2003; Kissling and Carl, 2008). As standard OLS regression models are not enough to establish statistical significance of variable prediction, we first checked the spatial patterns of observed mammalian species richness using Moran's I autocorrelation coefficients with 10 geographic distance classes (Blamires et al., 2008). According to Moran's I correlogram, regression residuals are likely to display substantial autocorrelation at small distances (Diniz-Filho et al., 2003; Melo et al., 2009). The first distance class higher than 0.1 in Moran's I coefficient was used to measure significant spatial structures in the model (Diniz-Filho and Bini, 2005; Blamires et al., 2008). If there was no detectable spatial autocorrelation (Moran's I spatial correlograms value is close to zero), then the species richness pattern could be explained by the predictors in the models (Zhao et al., 2006).

As many correlated variables can reduce the predictive power and interpretability (Morueta-Holme et al., 2010), we checked for multicollinearity between independent variables and removed those that were highly correlated ($R^2 \geq 0.70$) in our models. We conducted a two factor principal component analysis (PCA) on both groups of climatic and landscape metrics separately (Table S1) to reduce data volume. We used a Varimax-rotated principal component analysis (VrPCA), a procedure that permits a clear identification of major trends in the data, and pinpoints the variables that best represent them (i.e. those showing higher loadings in the main rotated factors; e.g. see Table S2). According to the 'broken stick' stopping criterion (Jackson, 1993), these major trends were captured by the first factor of the VrPCA, which described 77% of the variance in climate and 51% in landscape metrics. The highest factor loadings (≥ 0.90) for the first factor corresponded to 21 climatic predictors (Altitude, Avg tmean, Avg tmax, Avg tmin, Bio 1, Bio 2, Bio 4 to Bio 11, Bio 13 to Bio 19) and 11 landscape metrics (mean patch area, area-weighted mean patch area, division index, radius of gyration area-weighted mean, largest patch index, number of patches, patch density, patch richness, patch richness density, relative patch richness, and Shannon diversity). Among the correlated variable set we selected only important variables that might explain the mammal species richness patterns better. Therefore, multiple OLS regression models were used to analyze observed mammalian richness (total species, carnivores and non-carnivores) as a function of climatic variables, disturbance indices and landscape structure (Diniz-Filho et al., 2003; Griffith, 2003; Griffith and Peres-Neto, 2006; Rangel et al., 2006; Blamires et al., 2008). We used all possible combinations of predictors in the OLS models based on Akaike Information Criterion adjusted for small sample size (AIC_c). We used AIC_c for model choice by comparing all variable combinations and selected models with the lowest AIC_c values. The predictors of mammalian species richness were

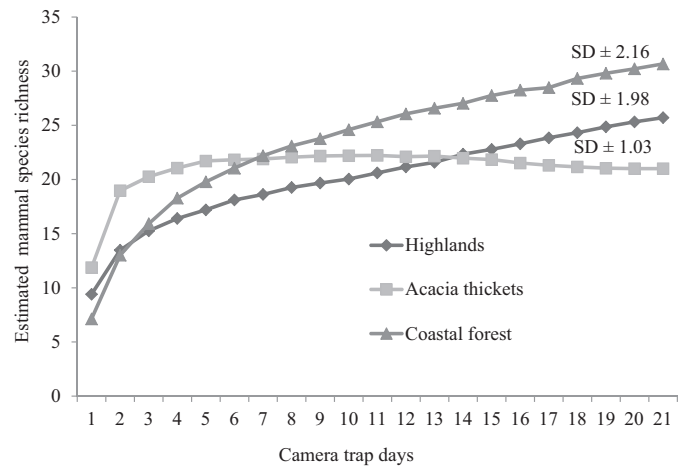


Fig. 2. Estimated total mammalian species richness using first order jackknife estimators across the three habitat types.

considered based on the highest importance values in multi-model inference (i.e. based on model weights). We followed the framework of Burnham and Anderson (2002) for model selection and computation of model weights. Model averaging was applied to estimate coefficients (Burnham and Anderson, 2002) of the top model predictors of richness ($\Delta AIC_c \leq 2$). We conducted all the spatial analyses using Spatial Analysis in Macroecology (SAM) software available at www.ecoevol.ufg.br/sam (Rangel et al., 2006).

3. Results

3.1. Richness pattern

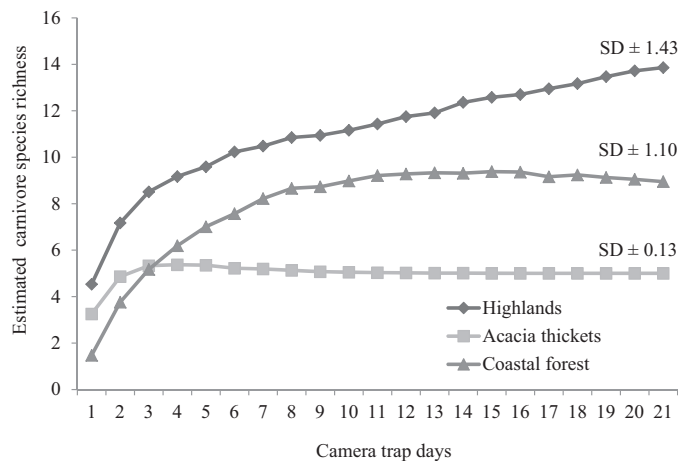
Twenty one days of camera trapping at 42 camera sites with 882 trap-nights yielded 2971 independent photo captures of 38 species of wild mammals. Fifteen carnivores and 23 non-carnivore mammalian species were photographed during the surveys (Table S3). Of the total species of carnivores, 10, 5 and 8 species were recorded in highland, Acacia thicket and coastal forest, respectively. For non-carnivore species, 10, 17 and 16 species were recorded in highland, Acacia thicket and coastal forest, respectively. The Jackknife Estimator of species richness curve showed that the estimated species richness appeared to stabilize towards the end of the sampling days. There was no significant difference in overall observed and mean expected mammalian species richness ($\chi^2 = 0.66$, $df = 2$, $P = 0.71$). The difference in observed and expected mammalian species richness was significant for coastal forest ($\chi^2 = 38.39$, $df = 20$, $P = 0.007$) but not for highland nor Acacia thicket ($\chi^2 = 30.28$, $df = 20$, $P = 0.06$; $\chi^2 = 7.99$, $df = 20$, $P = 0.99$). The overall estimated mammalian species richness was highest in coastal forest compared with the other two habitats (Acacia thicket/coastal forest, $U = 116.5$, $z = -2.60$, $P = 0.01$; highland/coastal forest, $U = 119$, $z = -2.54$, $P = 0.01$) while there was no difference between highland and Acacia thicket ($U = 200.5$, $z = -0.49$, $P = 0.62$; Fig. 2). However, carnivore richness was significantly lower in the coastal forest than highland ($U = 56$, $z = -4.13$, $P = 0.00$), and higher than Acacia thicket ($U = 46$, $z = -4.38$, $P = 0.00$), and carnivore richness was lowest in Acacia thicket to highland ($U = 20$, $z = -5.04$, $P = 0.00$; Fig. 3). For non-carnivores, mammalian richness was highest in coastal forest, followed by Acacia thicket and highland (highland/Acacia thicket, $U = 14$, $z = -5.18$, $P = 0.00$; Acacia thicket/coastal forest, $U = 127$, $z = -2.34$, $P = 0.02$; highland/coastal forest, $U = 61$, $z = -4.0$, $P = 0.00$; Fig. 4).

Table 2

Standardized ordinary least squares (OLS) regression models showing the predictors of mammalian species richness.

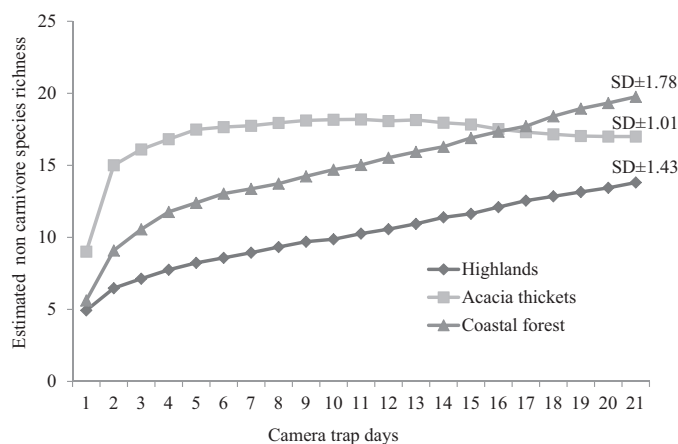
Response variable	Model predictors	Number of variables	Cond. Num.	AIC _c	Delta AIC _c	Model likelihood	Akaike weight
Climatic variables and richness groups							
Total species richness	Bio 13 + Avg tmax	2	3.375	225.04	0.00	1.00	0.36
Carnivore richness	Non-carnivores + Avg tmax	2	1.226	150.39	0.00	1.00	0.37
	Non-carnivore richness + Bio 3 + Avg tmax	3	1.625	150.93	0.54	0.76	0.28
	Non-carnivore richness	1	1	152.13	1.75	0.42	0.15
Non-carnivore richness	Carnivore richness + Bio 3 + Avg tmax	3	1.443	202.19	0.00	1.00	0.73
Landscape metrics							
Total species richness	Mean shape index + Division index	2	1.582	227.15	0.00	1.00	0.53
	Mean contiguity index + Mean shape index + Division index	3	1.738	228.94	1.79	0.41	0.22
Carnivores	Patch richness + Shannon diversity	2	2.214	151.96	0.00	1.00	0.45
	Shannon diversity	1	1	153.81	1.86	0.40	0.18
Non-carnivores	Mean shape index + Shannon diversity	2	1.358	202.66	0.00	1.00	0.39
	Mean shape index + Largest patch index	2	1.548	203.47	0.81	0.67	0.26
	Mean shape index	1	1	203.59	0.93	0.63	0.24

AIC_c, adjusted AIC for small sample size; Bio 3, isothermality (Bio 2/Bio 7); Bio 13, precipitation of wettest month (mm); Avg tmax, average monthly maximum temperature ($^{\circ}\text{C} \times 10$).

**Fig. 3.** Estimated carnivore species richness using first order jackknife estimators across the three habitat types.

3.2. Influence of climatic variables and mammal groups on richness

The variation in overall mammalian richness was not autocorrelated, showing no change of Moran's *I* coefficient across distances.

**Fig. 4.** Estimated non-carnivore species richness using first order jackknife estimators across a habitat gradient.

The first distance class was around 0.1 in Moran's *I* coefficients (Fig. 5). This can be clearly associated with little spatial variation in total richness across the distance classes in which distant areas do not have very distinct richness values. Overall, there was a low correlation among the final explanatory variables ($R^2 < 0.70$). We first inferred the internal structure of predictors of richness from a PCA (Table S1), which identified two factors that explained 89.8% and 71.3% of total variance for climatic and landscape variables, respectively. The top models, ranked by $\Delta\text{AIC}_c \leq 2$ and Akaike weight value, are shown in Tables 2 and 3. The variation in total mammalian species richness increased with precipitation of the wettest month (mm) (Bio 13) and average monthly maximum temperature. However, influences of individual predictors were much lower in the model. Average monthly maximum temperature negatively influenced carnivore richness, followed by isothermality (Bio 3). For non-carnivores, both average monthly maximum temperature and Bio 3 positively influenced richness. Carnivore and non-carnivore richness influenced each other in the model (Table 2).

3.3. Influence of landscape metrics on richness

Of all models tested for showing effects of landscape variables on total richness, the best supported was mean shape index showing positivity and division index showing negativity. These were followed by positive effects of mean forest contiguity index (Table 2). Moreover, the summed Akaike weight for forest contiguity was relatively small (0.29; Table 2). The summed Akaike weights (*w_i*) for each predictor and their model-averaged coefficients and standard errors (SE) are given in Table 3. Details of variables used

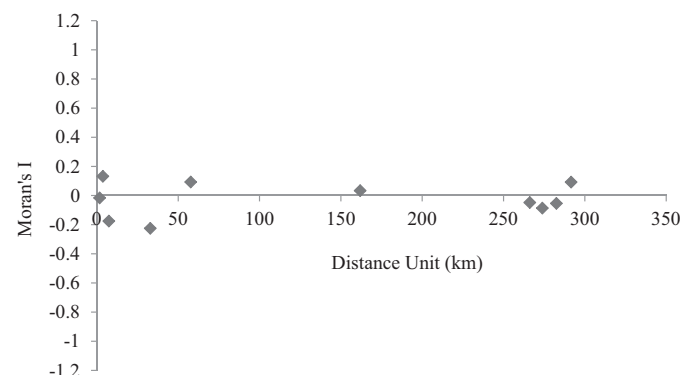
**Fig. 5.** Spatial correlograms for total mammalian species richness.

Table 3
Model average weights and coefficients of standardized ordinary least square (OLS) regression models for predictors of mammal species richness.

Response variable	Summed Akaike weight	Average coefficient	SE
Climatic variables			
Total mammal species richness			
Bio 13	0.702	0.318	0.122
Avg tmax	0.718	0.082	0.031
Carnivore species richness			
Non-carnivore species richness	0.856	0.181	0.071
Bio 3	0.39	−0.136	0.053
Avg tmax	0.766	−0.018	0.007
Non-carnivore species richness			
Carnivore species richness	0.88	0.707	0.248
Bio 3	0.90	0.574	0.199
Avg tmax	0.86	0.04	0.014
Landscape metrics			
Total mammal species richness			
Mean contiguity index	0.297	2.113	0.776
Mean shape index	0.965	9.262	3.298
Patch richness	0.239	−0.048	0.031
Division index	1	−2.228	3.693
Carnivore species richness			
Patch richness	0.695	−0.265	0.115
Mean shape index	0.288	0.231	0.411
Shannon diversity index	0.812	1.746	0.794
Non-carnivore species richness			
Mean shape index	0.989	8.047	2.48
Shannon diversity index	0.498	−2.249	0.77
Largest patch index	0.368	0.026	0.013

Bio 3, isothermality (Bio 2/Bio 7); Bio 13, precipitation of wettest month (mm); Avg tmax, average monthly maximum temperature ($^{\circ}\text{C} \times 10$).

for initial analysis are given in Table S2. For carnivore richness, habitat diversity was the most important positive predictor, followed by patch richness negatively. Non-carnivore richness was best explained by mean shape index positively. Shannon diversity and largest patch had secondary negative and positive influences on non-carnivore richness, respectively. However, the variable was prominent in highly ranked multivariate models, indicating its effects were mediated in the presence of other predicting variables.

4. Discussion

Mammalian richness is often associated with temperature and rainfall (Schall and Pianka, 1978; Owen, 1990; Zhao et al., 2006; O'Hara and Tittensor, 2010). Climatic factors and landscape metrics revealed species richness patterns in the habitat-mosaics of South Africa. As expected, our results demonstrated that mammalian richness was lower in habitats which are prone to higher disturbance. The estimated richness was highest in the lowland coastal forest of the protected area setting due to forest continuity and high quality habitat (Rowe-Rowe and Taylor, 1996). Carnivore richness was lower in the coastal forest than highland, and higher than the *Acacia* thicket due to the prevalence of many medium-sized carnivores in the highland and the absence of large predators. The presence of large predators in the coastal forest could have caused the absence of medium-sized carnivores, and thus the lower carnivore richness, because of interspecies competition (Ritchie and Johnson, 2009). In the *Acacia* thicket area, carnivore richness was very low. This is likely to be because of the fragmented mono-habitat, i.e. *Acacia* thicket is disturbed by human-introduced invasive species such as domestic dogs and cats, and may also be influenced by retaliatory killing of carnivores for livestock loss. Large carnivores are affected by habitat loss that can lead to high extinction rates (Karanth et al., 2004). Large carnivores appeared to exhibit a more pronounced response to habitat disturbance (Msuha

et al., 2012); as such, leopard (*Panthera pardus*) and spotted hyena (*Crocuta crocuta*) were only recorded in the coastal forest of the protected area. Small rodents were generally more abundant in the highland, which can support a substantial population of medium-sized carnivores (Bowland, 1990; Bowland and Perrin, 1993) which is likely to have a major influence on the distribution and habitat use of these carnivores.

Coastal forest supported higher estimated non-carnivore richness, which was probably because of habitat protection and habitat connectivity with the adjacent forested area. This would have supported a large number of ungulate species. *Acacia* thicket also had substantially more non-carnivore species. We speculate that this could be because of the introduction of some of the ungulates to this habitat. Overall, the total number of both mammalian species and non-carnivore species was higher in coastal forest areas. A previous survey indicated that overall mammalian richness was generally higher in the north-eastern part (coastal forest) of the KwaZulu-Natal province although carnivore-rich areas are found in the north-west and south-west (highland) portion (Rowe-Rowe and Taylor, 1996). The higher species richness in lowland coastal forests is not only an artefact of the species presence in protected areas (Kiffner et al., 2014) but was also related to the location of the richer Lowveld bioregion and the northern Coast lowlands (Rowe-Rowe and Taylor, 1996). The low carnivore richness in the disturbed *Acacia* thickets suggests that carnivores are highly subject to increasing anthropogenic pressure.

4.1. Climatic predictors of species richness

We found that average monthly maximum temperature had a substantially higher predictive power relative to all other variables for explaining the total species richness, and carnivore and non-carnivore richness patterns. A significant negative effect of temperature occurred for carnivores only, while non-carnivores showed a positive response to temperature because temperature enhances productivity of vegetation (Herfindal et al., 2005; Pettorelli et al., 2009; Sandom et al., 2013) and plant productivity and quality predict general patterns of herbivore diversity (Olff et al., 2002). Rowe-Rowe and Taylor (1996) observed highest species richness in the warmest and most heterogeneous (vegetation) bioregions. Often the wetter and warmer regions are the most productive for plant growth (Moles et al., 2009; Olff et al., 2002). Correspondingly, non-carnivore richness increased with isothermality. Further, our richness variables included herbivores such as ungulates and primates that are generally dependent on forage quality and plant productivity. However, given that most of the models included temperature, it seems reasonable to conclude that it is related to overall mammalian species richness, and the model-averaged results suggest that it is indeed one of the most important variables.

Precipitation determines plant productivity and quality (Reich et al., 1997; Walker and Langridge, 1997). Generally, herbivore community structure and distributions are strongly influenced by plant quality and productivity (Belovsky, 1987; Owen-Smith, 2002; Wilkin and Mayo, 2013). Many studies have showed that herbivore richness is related to precipitation (Rosenzweig, 1995; Danell et al., 1996; Eronen et al., 2010), which supports our finding that precipitation of the wettest month was the major predictor of total mammalian richness. The non-carnivore category was mainly dominated by herbivores, and generally carnivore richness is related to herbivores in the food web. However, the combined effects of climate were considerably lower for determining carnivore richness, indicating that these factors played less important roles at higher trophic levels (Sandom et al., 2013). The mesocarnivore richness was greater in the highland where temperatures are lowest. Thus, carnivores exhibited a negative response to this

environmental variable. When including non-carnivore richness as the explanatory variable to predict carnivore richness, our model effectively explained variance in both richness categories along with the environmental variables. This effect could be directly linked with prey availability and diversity for carnivores to avoid competitive exclusion, and this in turn may have a productivity effect through an increase in prey abundance (Kiffner et al., 2015). However, we believe that the diverse range of carnivores facilitates higher (non-carnivore) prey richness considering effects of bioclimatic variables. The effect of human influence on both predator and prey richness were generally weak at the scale studied.

4.2. Effect of landscape metrics on species richness

The total mammalian species richness decreased with increasing division of habitat, indicating that increase in small fragmented patches in a landscape causes detrimental effects on mammal distribution and populations. Conversely, habitat fragmentation increases edge habitats, which are considered as favourable for some mammals as they contain a combination of diverse structures and thus increases the distribution range of species in a landscape (Lidicker, 1999). Mean shape index quantifies patch complexity where complex narrow shape features of patches decrease core areas and increase edge habitats compared with normal shapes like circles or squares (Forman, 1995; Fleishman et al., 2002; Martinez-Morales, 2005). The total mammalian and non-carnivore species richness were positively linked to greater mean shape complexity as this provided more complex edge habitats for usage by several species; however, it was a weak positive predictor of carnivore richness. Studies have shown that changes in microclimate, vegetation structure and food availability along forest edges reduce populations of many interior-forest dependent vertebrates (Wilcove, 1985; Robbins et al., 1989). Therefore, many species are sensitive to patch shape complexity in fragmented or mosaic landscapes.

The positive response of mammalian richness towards habitat contiguity supports the fact that larger patches of habitat contain a higher number of species than smaller patches (MacArthur, 1967). Because disconnected patches prevent dispersal patterns, maintaining contiguity of high quality patches is essential to maintain energy flow, nutrient and gene flow. Moreover, in fragmented systems the habitat contiguity depends on patch connectivity. In our study area, highland and *Acacia* thicket habitats have been fragmented for agriculture purposes and other developmental activities resulting in more isolated habitat patches and an increasingly fragmented landscape. In the future, unprotected habitats will face more habitat fragmentation, and consequently inadequate contiguous habitat patches will not support viable animal populations. Conservation agencies should increase the level of community participation in establishment of community wildlife-conservation areas and provide incentives and compensation for wildlife damage on private properties. Therefore, strategies for biodiversity conservation and management should not only target protected areas but also managed land which can also increase the availability of suitable habitat that host significant wildlife species.

Higher spatial heterogeneity can significantly affect animal dispersal through presence of large numbers of land-cover types. Shannon's Diversity Index was identified as the main predictor of carnivore richness. We believe that this was mainly due to the high mesocarnivore richness in the heterogeneous highland habitat, which also probably has a large abundance of small mammals as prey in the highland (Bowland and Perrin, 1993). The ecological effects of structural attributes of habitat heterogeneity may vary greatly between species groups and all of these depend upon how heterogeneity or fragmentation is considered (Tews et al.,

2004). A previous study indicated that mammalian species richness decreases with increasing habitat heterogeneity (Sullivan et al., 2001). Response of herbivores to habitat fragmentation is often regarded as unpredictable due to different effects on diverse trophic levels (Kruess and Tschardtke, 1994). Therefore, it is possible that we did not predict a linear relationship of non-carnivore richness with habitat diversity. Our results offer interesting insights into how carnivore and non-carnivore species richness respond to landscape composition at small scales.

Carnivores responded to patch richness negatively, probably as patch richness did not account for the relative proportion or abundance of each patch type where rare and common patch types are treated equally to richness (McGarigal et al., 2002). Patch richness can be related to species richness if many species are supported by a single patch type. Generally, larger areas support high species richness as there is more heterogeneity compared with smaller areas (MacArthur and Wilson, 1967). The decrease in patch size could lead to populations susceptible to local extinction by reducing resource availability and increasing edge effects (Stratford and Stouffer, 1999; Fleishman et al., 2002; Martinez-Morales, 2005). Although increasing patch size was a weak predictor in the model, non-carnivore richness showed a positive response to the largest patch. The largest patches can enhance the connectivity of habitats in a landscape thereby supporting higher mammalian richness and dispersal abilities of animals in a landscape.

5. Conclusion

Our study highlights that the best predictors of mammalian richness are bioclimatic variables, particularly temperature, isothermality and precipitation. Further, our results suggest that temperature and rainfall limit species richness in sub-tropical habitats of South Africa. The continuous coastal forest supported high species richness, although highlands supported mesocarnivore richness comparatively more than coastal forest. Mammal conservation outside protected areas relies on efforts to understand the effect of human activities on mammal ecology, and how restoration efforts may mitigate negative impacts. The increase in small patches in our landscape could cause serious deleterious effects on mammalian richness. The effects of mean shape complexity on mammalian species richness indicate that edge habitats are particularly important for non-carnivores. Therefore, it is necessary to preserve larger and complex-shaped patches within the matrix, as this management strategy can increase landscape connectivity, thus favouring inter-patch mammal movements, as well as key ecological dynamics for diversity maintenance of fragmented landscapes (Fahrig, 2003). Our findings show that large contiguous patches and forest connectivity are important for maintaining mammal populations. If natural habitats are not assigned value, the ongoing agricultural intensification will lead to heavy fragmentation of natural habitats into small islands and isolated patches, thus exacerbating the effect of habitat loss over a range of mammalian species. The identification of climatic and landscape patterns is important to facilitate future landscape management for mammal conservation in forest-mosaics. We recommend that future studies use ground-truthing methods and focus on the impact of habitat fragmentation on mammal richness at larger landscape scales and especially in habitats facing varying degrees of disturbance.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2015.07.011>

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