

# Variation in mammal species richness and relative abundance in the Karoo<sup>§</sup>

Zoë Woodgate<sup>1\*</sup>, Greg Distiller<sup>2</sup> and Justin O’Riain<sup>1</sup>

<sup>1</sup> Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

<sup>2</sup> Statistics in Ecology, Environment and Conservation, Department of Statistical Science, University of Cape Town, Cape Town, South Africa

\* Corresponding author, email: [zwoodgate@outlook.com](mailto:zwoodgate@outlook.com)

Understanding how climate change and land transformation may impact the distribution and diversity of wildlife species requires landscape-level foundational biodiversity surveys. The Karoo BioGaps Project aims to provide such data and to support the scientific assessment for shale gas development projects in the Karoo basin. In this paper we present the findings of the BioGaps mammal survey, which recorded medium and large mammals across twenty-five 1 km × 1 km sampling sites within the proposed fracking footprint using camera trapping techniques. We use sample rarefaction curves, non-parametric species richness estimators and non-metric multidimensional scaling plots to explore both species richness and community structure. We also used a generalised linear model to investigate how species diversity varies with both site-specific and landscape-level predictors. A total of 38 species were recorded at the majority of sites. Longitude ( $z = 4.018$ ,  $p = 0.0005$ ) emerged as the best predictor of species diversity across the study area, which we suggest is linked to the clear east–west aridity gradient. Together these results reveal the cosmopolitan distribution of the mammal taxa in the Karoo and could be used to inform decision-making linked to mining activities in the area.

**Keywords:** Karoo, mammals, shale gas

**Online supplementary material:** Supplementary information for this article is available at <https://dx.doi.org/10.2989/10220119.2018.1522513>

## Introduction

In order to meet the demands of an increasing human population, extensive areas of land have been transformed for food production, mining and housing with a concomitant loss of ecological processes and biodiversity (du Toit and Cumming 1999; Hunter and Gibbs 2007; Hughes et al. 2008; Laurance et al. 2014; Mann et al. 2015; Meng 2017). In addition, climate change is predicted to impact contemporary ecosystems by further fragmenting natural landscapes and reducing wildlife populations (Magurran et al. 2010; Boshoff et al. 2016). Understanding how current and proposed land use threats will affect the distribution and diversity of wildlife species requires foundational biodiversity information (Hunter and Gibbs 2007; Hilty et al. 2012; Steenweg et al. 2017).

In South Africa, the majority of natural land transformation is attributed to agriculture and urbanisation (Roux et al. 1981; Rouget et al. 2003). Approximately 80% of South Africa’s total land area is under both permanent crops and pastures (World Bank 2014). Recently, the Karoo, a semi-arid region that covers more than 40% of the country’s interior, has been earmarked for several large-scale infrastructure development projects, including shale gas exploration and uranium mining (Hoffman and Cowling 1990; Mucina and Rutherford

2006; Todd et al. 2017). The natural gas predicted to be present in the Karoo basin is unconventional in that it is trapped in large shale formations and can only be released by the controversial process of hydraulic fracturing (hereafter ‘fracking’) (Scotchman 2016; Meng 2017; Schreiner and Snyman-van der Walt 2017). Concerns have been raised over the potentially negative impact this process will have on the region’s agricultural activities (mostly free-ranging livestock), freshwater resources and general ecology (Vermeulen 2012; Mayer 2016; Scholes et al. 2016; Christenson et al. 2017; Todd et al. 2017). In particular, the cumulative effects of fracking may greatly reduce the suitability of the environment for species that persist in these systems (Scholes et al. 2016; Todd et al. 2017). These concerns, in addition to those on the paucity of information on sensitivities, vulnerabilities and risks to the Karoo, were detailed in the Strategic Environmental Assessment compiled by the government (Scholes et al. 2016). This assessment highlighted the general lack of biodiversity data for the Karoo and led to the South African National Biodiversity Institute (SANBI) initiating a three-year ‘BioGaps’ project.

The primary aim of the BioGaps project is to systematically collect foundational biodiversity data across the proposed

<sup>§</sup> This article is from the ‘Karoo Special Issue: Trajectories of Change in the Anthropocene’.

Shale Gas Exploration Area (SGEA). To accomplish this a consortium of institutions has been commissioned to conduct surveys on each of the 12 representative taxonomic groups, which together comprise most of the floral and faunal communities of the Karoo. In this paper we report on the medium- to large-mammal (>0.5 kg) component of the BioGaps project. Approximately 176 mammal species (including bat and rodent species) are assumed to have all or part of their distribution in the proposed fracking area (Todd et al. 2017). The Karoo-endemic riverine rabbit (*Bunolagus monticularis*) is particularly vulnerable to land-use changes (Hughes et al. 2008) and is currently listed as Critically Endangered in the South African Red Data Book for mammals (Child et al. 2016).

Historically, the Karoo region was host to large groups of nomadic equids and antelope, with their itinerant predators (Dean and Milton 1999; Beinart 2004). However, as European settlers moved inland most larger species were extirpated, with fencing impeding smaller migratory species, such as springbok (Dean and Milton 1999). Today, medium and large mammal species continue to face a myriad of threats in the Karoo, including but not limited to, direct persecution by humans, exploitation and habitat degradation (Seymour and Dean 1999; Hoffman and Zeller 2005; O'Brien et al. 2010; Nattrass and Conradie 2015). Despite these threats there is recent evidence that extensive livestock farming areas in both the Little and Great Karoo have similar levels of species richness to adjacent protected areas (Mann et al. 2015 and Drouilly et al. 2018, respectively). Low human presence, the eradication of most large carnivores and provisioning of large numbers of domestic livestock may all favour the persistence of small and medium-sized carnivore and antelope species on farmland.

Globally, gradients in biodiversity and productivity are driven by a variety of environmental factors, including but not limited to, broad climatic differences (Willig et al. 2003; Mannion et al. 2014) with, for example, a decrease in biodiversity associated with increasing distance (i.e. latitude) from the tropics (Willig et al. 2003). Longitudinal shifts in biodiversity are also apparent but are less obvious than latitudinal shifts and primarily linked to complex aridity gradients and water availability with respect to topography (Qian et al. 1998; Lite et al. 2005). These aridity gradients are important in determining plant species richness (Yan et al. 2015) with more mesic areas having both higher productivity and higher plant species richness (Gould 2000; Mittelbach et al. 2001; Gillman and Wright 2006). In the semi-arid Karoo primary productivity is low and this has largely restricted agricultural activities to extensive livestock farming (predominantly sheep) (Dean and Milton 1999; Beinart 2004). Pastoralism has degraded the vegetation of the Karoo while retaining broad-scale biodiversity and ecological integrity (Scholes et al. 2016). Few studies have explored the impacts of this agricultural activity on the fauna, but it is widely accepted that large carnivores and antelope have been extirpated from much of the Karoo rangelands (Dean and Milton 1999; Beinart 2004).

In this study we utilised camera trapping to evaluate medium and large mammal species richness at multiple sites across the Karoo. Camera traps have been shown to be an effective method for detecting medium- and

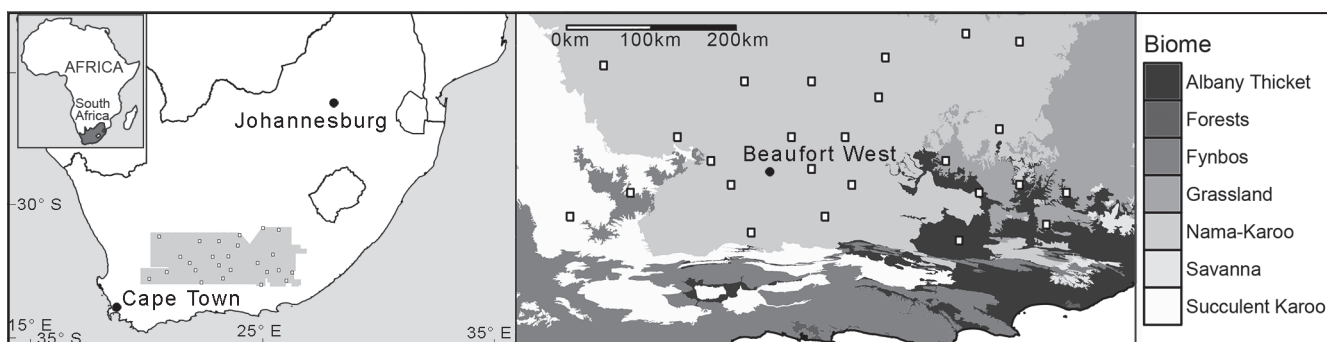
large-sized mammals across a range of habitat types, including the semi-arid region of South Africa (Burton et al. 2015; Mann et al. 2015; Drouilly et al. 2018). We also investigate the influence of both site-specific and landscape-level predictors on mammalian species richness in the Karoo. Predictors include the normalised difference vegetation index (NDVI), annual precipitation, relative abundance of livestock and terrain roughness, all of which have been shown to influence mammal species richness and distribution (Waide et al. 1999; Scholes et al. 2002; Lite et al. 2005; Todd 2006; Nunn and Puga 2012; Lagesse and Thondhlana 2016). Finally, we explore whether the longitudinal/latitudinal positioning of sites, which integrates abiotic and biotic processes at the landscape level (Qian et al. 1998; Willig et al. 2003; Lite et al. 2005), predicts species richness patterns within the Karoo. We predicted that mammalian species diversity would be positively influenced by rainfall (Lite et al. 2005), NDVI (Waide et al. 1999; Mittelbach et al. 2001) and topographic heterogeneity (terrain roughness) (Karanth et al. 2009; Nunn and Puga 2012). In addition, we predicted that species richness would decrease along a longitudinal gradient from east to west (Andrews and O'Brien 2000; Scholes et al. 2002; Kooyers et al. 2014) and be negatively impacted by intensive livestock farming (Todd 2006; Kinnaird and O'Brien 2012; Lagesse and Thondhlana 2016).

These findings will improve our understanding of the current distribution of wildlife in the Karoo and, together with data from other taxa, will ultimately allow for the mapping of biodiversity vulnerabilities, which can be used to inform decision-making and set regional limits of acceptable anthropogenic disturbance within the Karoo. These data will also provide an important baseline for monitoring long-term changes in response to climate change proposed for the Karoo region.

## Methods

### Study area

The proposed SGEA covers approximately 120 000 km<sup>2</sup> of the Karoo, an extensive semi-arid region of South Africa that spans four provinces (Western Cape, Northern Cape, Eastern Cape and Free State) (Figure 1; Hoffman and Cowling 1990; Todd et al. 2017). In order to document foundational biodiversity information across the SGEA, as part of the SANBI Biogaps project, 60 sampling sites were selected using Latin hypercube sampling implemented in the *clhs* package for R (Minasny and McBratney 2006; R Development Core Team 2011; Roudier 2018). This approach seeks to capture the environmental gradients within the SGEA, while avoiding spatial autocorrelation between sites. Budgetary, logistical and temporal constraints unique to each taxon group resulted in the random subsampling of these 60 sites. The mammal taxon group was primarily limited by the availability of camera traps and the need to leave cameras at each site for a minimum of 30 consecutive days. Here we present results from twenty-five 1 km<sup>2</sup> sites within the SGEA. Eighteen sites fall within the second-largest biome in South Africa, the Nama-Karoo, characterised by dwarf shrubland and rugged topography (Mucina and Rutherford 2006). The remaining



**Figure 1:** Map of the shale gas exploration area (delimited by the shaded grey zone) and location of all 25 sites (white squares), within which the 1 km<sup>2</sup> sampling sites were located. Insert shows the sites in relation to the region's biomes, as classified by Mucina and Rutherford (2006)

seven sites included the Succulent Karoo (2), Savanna (2) and Grassland biomes (3) (Supplementary Table S1). All but one of the sites were located on privately-owned commercial livestock farms primarily used as rangeland for grazing by domestic livestock (Supplementary Table S1; Roux et al. 1981). The final site was located within the Plains of the Camdeboo Nature Reserve, which includes both reintroduced large ungulates, such as Cape mountain zebra (*Equus zebra zebra*) and nguni cattle (*Bos taurus*).

#### **Sampling mammal diversity and relative abundance using camera traps**

A total of nine camera traps were deployed at each site. Four cameras were used to sample the four main habitat types identified across all sites, namely plateau/mountain, steep slopes, riverbeds and plains. Camera stations were placed randomly within each habitat type in places that included signs of animal presence (e.g. trails and scat) to increase the probability of detecting the target species (Burton et al. 2015). On average, cameras were approximately 400 m apart. The five other camera traps were used specifically to detect the elusive riverine rabbit. Previous research suggests that riverine rabbits have a mean home range size of 400 m<sup>2</sup> and are more likely to be detected in or adjacent to dry riverbeds (Duthie 1989). Consequently, we placed the five camera traps over an area of roughly 400 m<sup>2</sup> on the edge of dry riverbeds. In total, 225 cameras were deployed across all 25 sites.

All camera traps were secured to a metal stake at a height of approximately 30–50 cm. A 1-minute interval between trigger events was selected, with each trigger event comprising three consecutive photographs to improve the identification of the photographed animal. Cameras were operational for a minimum of 30 consecutive days to improve the probability of detecting rare species (e.g. riverine rabbits) and species with large home ranges (e.g. leopard [*Panthera pardus*]) that would traverse the study site only rarely. Sampling of the 25 sites was divided into four separate surveys from September 2016 (spring) to May 2017 (autumn). Seven to 10 sites were completed during each survey, starting at the middle-most site (located close to Beaufort West). Subsequent surveys added sites from both east and west of Beaufort West. While this does introduce seasonal variation, few of the remaining medium and large mammal species in the Karoo exhibit seasonal

movement or behavioural patterns (Dean and Milton 1999; Drouilly et al. 2018). We therefore did not anticipate that seasonality would impact the presence of medium and large mammals on farmland within the Karoo.

#### **Analyses**

Camera traps within a given site were not considered to be spatially independent. We therefore standardised sampling effort across all sites by pooling all the photographs from the nine camera stations for each site. Independent captures were defined by 30-minute intervals between photographs of the same species for the entire site, or by being an obviously new individual, such as when individual markings or features (e.g. abnormal horn shape) allowed for individual identification (Tobler et al. 2008). Images were processed using Camera Base® software (Tobler 2007). Livestock (e.g. sheep), domestic (e.g. dog) and non-native (e.g. fallow deer [*Dama dama*]) mammal species were excluded from analyses, as were small mammals weighing <0.5 kg (e.g. rodents), which are not reliably detected using camera traps. Cape clawless otter (*Aonyx capensis*) was also excluded from the analysis as its semi-aquatic lifestyle makes terrestrial camera trapping an unsuitable method for detecting this species (Okes and O'Riain 2017). For each target species at each site, the relative abundance index (RAI) was calculated as the number of captures per 100 trap nights (Table 1). Whilst RAIs have been criticised for not incorporating detection heterogeneity between species, they can be useful in making broad-scale inferences and species-level comparisons within single surveys (Sollmann et al. 2013; Burton et al. 2015; Ellis et al. 2017; Hofmeester et al. 2017).

To determine whether our sampling protocol provided sufficient temporal and spatial sampling effort, we used the vegan package (Oksanen et al. 2018) in the R statistical environment to compile sample-based rarefaction curves, with 1 000 randomisation runs (Colwell et al. 2004; Tobler et al. 2008; Gotelli and Colwell 2011). In addition, to account for undetected species, we computed non-parametric species richness estimators (i.e. Chao 1, first-order and second-order Jackknife and bootstrap) (Colyn et al. 2017). To visualise patterns in species assemblages among sites, we again used the vegan package to construct non-metric multidimensional scaling (NMDS) ordinations (Woese et al. 1990), using the Jaccard (presence/absence) similarity

**Table 1:** List of species photographed ( $n = 38$ ) during all four surveys conducted from September 2016 to May 2017 throughout the Shale Gas Exploration Area. Included is the total number of detections, species relative abundance index (RAI), the number of sites where each species was detected (out of the 25), and regional Red List status (Child et al. 2016)

| Common name                | Species  | Total number of detections | RAI      | Number of sites | Regional Red List status |
|----------------------------|--|----------------------------|----------|-----------------|--------------------------|
| Aardvark                   | <i>Orycteropus afer</i>                                      | 105                        | 239.32   | 20              | Least Concern            |
| Aardwolf                   | <i>Proteles cristata</i>                                     | 38                         | 90.26    | 11              | Least Concern            |
| African wild cat           | <i>Felis lybica</i>  | 11                         | 26.50    | 3               | Least Concern            |
| Bat-eared fox              | <i>Otocyon megalotis</i>                                     | 141                        | 335.80   | 12              | Least Concern            |
| Black-backed jackal        | <i>Canis mesomelas</i>                                       | 74                         | 181.31   | 15              | Least Concern            |
| Black-footed cat           | <i>Felis nigripes</i>  | 3                          | 7.54     | 2               | Vulnerable               |
| Blesbok                    | <i>Damaliscus pygargus phillipsi</i>                         | 157                        | 334.88   | 3               | Least Concern            |
| Bushbuck                   | <i>Tragelaphus sylvaticus</i>                                | 85                         | 192.50   | 3               | Least Concern            |
| Bushpig                    | <i>Potamochoerus larvatus</i>                                | 18                         | 42.50    | 3               | Least Concern            |
| Cape fox                   | <i>Vulpes chama</i>  | 32                         | 77.57    | 8               | Least Concern            |
| Cape mountain zebra        | <i>Equus zebra zebra</i>                                     | 7                          | 17.50    | 1               | Vulnerable               |
| Caracal                    | <i>Caracal caracal</i>                                       | 21                         | 44.32    | 11              | Least Concern            |
| Chacma baboon              | <i>Papio ursinus</i>   | 868                        | 1 567.24 | 10              | Least Concern            |
| Common duiker              | <i>Sylvicapra grimmia</i>                                    | 939                        | 2 096.14 | 16              | Least Concern            |
| Hare spp.                  | <i>Lepus saxatilis</i> and <i>Lepus capensis</i>             | 776                        | 1 697.83 | 23              | Least Concern            |
| Eland                      | <i>Taurotragus oryx</i>                                      | 42                         | 63.48    | 2               | Least Concern            |
| Gemsbok                    | <i>Oryx gazella</i>  | 24                         | 57.12    | 4               | Least Concern            |
| Genet spp.                 | <i>Genetta tigrina</i> and <i>Genetta genetta</i>            | 70                         | 170.18   | 12              | Least Concern            |
| Greater kudu               | <i>Tragelaphus strepsiceros</i>                              | 1 002                      | 2 179.99 | 19              | Least Concern            |
| Grey mongoose spp.         | <i>Herpestes ichneumon</i> and <i>Galerella pulverulenta</i> | 20                         | 49.15    | 8               | Least Concern            |
| Grey rhebok                | <i>Pelea capreolus</i>                                       | 82                         | 192.72   | 6               | Near Threatened          |
| Ground Squirrel            | <i>Xerus inauris</i>   | 10                         | 24.39    | 1               | Least Concern            |
| Impala                     | <i>Aepyceros melampus</i>                                    | 241                        | 509.40   | 3               | Least Concern            |
| Klipspringer               | <i>Oreotragus oreotragus</i>                                 | 2                          | 4.76     | 1               | Least Concern            |
| Marsh mongoose             | <i>Atilax paludinosus</i>                                    | 32                         | 73.75    | 5               | Least Concern            |
| Meerkat                    | <i>Suricata suricatta</i>                                    | 153                        | 375.95   | 13              | Least Concern            |
| Porcupine                  | <i>Hystrix africaeaustralis</i>                              | 116                        | 272.21   | 21              | Least Concern            |
| Red hartebeest             | <i>Alcelaphus buselaphus caama</i>                           | 19                         | 42.02    | 4               | Least Concern            |
| Rock hyrax                 | <i>Procavia capensis</i>                                     | 6                          | 15.48    | 3               | Least Concern            |
| Smith's red rock rabbit    | <i>Pronolagus rupestris</i>                                  | 22                         | 53.26    | 6               | Least Concern            |
| Southern mountain reedbuck | <i>Redunca fulvorufula fulvorufula</i>                       | 317                        | 681.18   | 9               | Endangered               |
| Springbok                  | <i>Antidorcas marsupialis</i>                                | 445                        | 1 065.87 | 12              | Least Concern            |
| Springhare                 | <i>Pedetes capensis</i>                                      | 51                         | 116.59   | 2               | Least Concern            |
| Steenbok                   | <i>Raphicerus campestris</i>                                 | 548                        | 1 242.78 | 23              | Least Concern            |
| Striped polecat            | <i>Ictonyx striatus</i>                                      | 24                         | 60.29    | 9               | Least Concern            |
| Vervet monkey              | <i>Chlorocebus pygerythrus</i>                               | 851                        | 1 848.91 | 13              | Least Concern            |
| Warthog                    | <i>Phacochoerus africanus</i>                                | 185                        | 426.67   | 3               | Least Concern            |
| Yellow mongoose            | <i>Cynictis penicillata</i>                                  | 13                         | 32.55    | 7               | Least Concern            |

index. We used the 'ordisurf' function from the vegan package to contour environmental variables in the ordination space; 'ordisurf' fits smooth surfaces using generalised additive models (Oksanen et al. 2018).

We then computed species diversity for all 25 sites by calculating the Shannon's diversity index ( $H$ ) as  $H = -\sum_{i=1}^S (p_i \ln p_i)$ , where  $p_i$  is the proportion of species  $i$  relative to the total number of species present in the community (Shannon 1948). As the Shannon diversity index is not itself a 'true' diversity estimate, we calculated the effective number of species (ENS), which is representative of the number of equally-abundant species in a community, where  $ENS = e^H$  (Jost 2006; Tuomisto 2010). We thereafter used generalised linear models (GLMs) to investigate how variation in the ENS was influenced by both site-specific (NDVI, livestock RAI and biome) and landscape-level (average annual precipitation, latitude, longitude and terrain

roughness) predictors (Table 2). Covariate values were extracted from each camera trap position in the free GIS software QGIS (QGIS Development Team 2018), and then averaged to produce a single value for each site. Predictors were tested for correlation using the Pearson's product-moment correlation test and single-factor analysis of variance (ANOVA). The NDVI, average annual precipitation and longitude were found to be highly correlated ( $r > 0.6$ ), as was biome and longitude ( $P > 0.5$ ). These covariates were subsequently modelled separately.

In our study we fitted GLMs specifying a gamma error distribution and the identity link function. Diagnostic plots of fitted linear models showed signs of non-constant variance. The gamma distribution was thus preferred over the standard Gaussian distribution as it is useful in analysing non-negative data that is continuous and positively skewed. The most parsimonious model was selected according to



**Table 2:** Description of the site-specific and landscape-level covariates estimated for each sample site (1 km<sup>2</sup>) in the Shale Gas Exploration Area. The index describes the type of data used to derive each covariate. The predicted effect (+/-) is how we predict the covariate will affect the effective number of species (ENS). Data source refers to the source used to estimate the covariate for each site. NDVI = normalised difference vegetation index

| Covariate          | Index   | Predicted effect | Data source  |
|--------------------|---|------------------|--|
| Biome              | Nama-Karoo, Succulent Karoo, Grassland or Savanna   | +/-              | 2006 Vegetation Map of South Africa, Lesotho and Swaziland (Mucina and Rutherford 2006)                      |
| NDVI               | Averaged 16-day composite NDVI from 2016 to 2017, averaged across all nine camera trap locations per site           | +                | 250 m MODIS NDVI, a product of NASA (Didan 2015)   |
| Rainfall           | Average monthly rainfall (mm) averaged from 2013 to 2017, averaged across all nine camera trap locations per site   | +                | The Tropical Rainfall Measuring Mission (TRMM_3H25) monthly precipitation data set (Takayabu and Shige 2011) |
| Terrain roughness  | Terrain ruggedness index calculated from ASTER GDEM (2011), averaged across all nine camera trap locations per site | +                | ASTER GDEM Version 2   |
| Longitude          | Midpoint of site (latitude, decimal degrees)  | +/-              | Recorded on site by researcher with a handheld GPS   |
| Latitude           | Midpoint of site (longitude, decimal degrees)   | +/-              | Recorded on site by researcher with a handheld GPS   |
| Livestock presence | The total relative abundance (RAI) of all livestock species at each site  | -                | Extracted from camera trapping photographs   |

the Akaike information criterion corrected for small sample sizes (AICc), using the package MuMin (Bartoń 2018) (Table 3).

## Results

The camera trap survey yielded a total of 8 813 camera-trap nights for 196 cameras or 1 024 independent camera-trap nights for all 25 sites. Twenty-nine cameras (12.9%) experienced data loss due to disturbance or software malfunction and were thus excluded. A total of 38 mammal species were recorded (Table 2) across all sites with 9 503 independent photographs, of which 6 404 were of the target wildlife species and 2 221 were of livestock. Independent captures of target species that were both indistinguishable from photographs and closely related (such as small and large grey mongoose) were treated as single species to prevent falsely inflating species richness (Table 2, Supplementary Table S2). Species accumulation curves for both the total number of trapping nights and sites reached an asymptote after approximately 28 camera trappings days (Supplementary Figure S1) and across sites after sampling seven of the 25 sites (Supplementary Figure S1). Non-parametric species richness estimators stabilised around 20–22 sites (Figure 2). Chao estimated the lowest number of target species in the study region (38.44, SD 2.2), whereas Jackknife2 estimated the highest (40, SD 1.7). Consequently, our sampling effort ranged from 95% (observed species/Chao) to 98.8%, (observed species/Jackknife2).

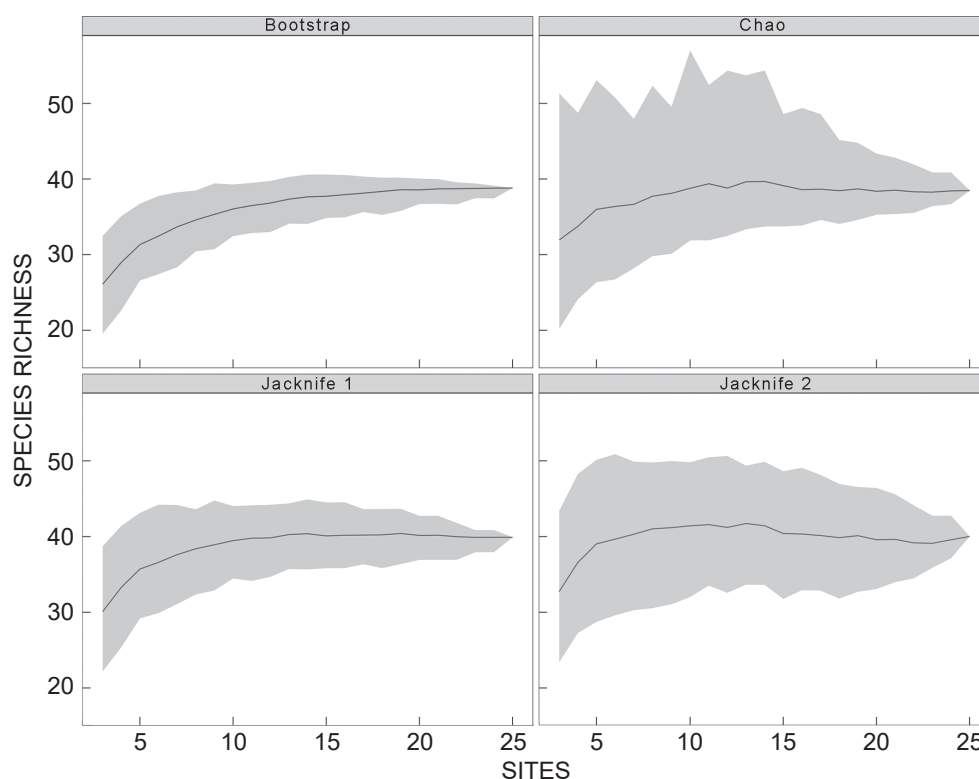
A total of 38 wild, target mammal species was recorded (Supplementary Table S2). The average number of target mammal species per site was 13.08, with the highest being 21 and the lowest six (Supplementary Table S1). This excluded one extralimital species, fallow deer, which was detected at two sites. Greater kudu (*Tragelaphus strepsiceros*) had the highest number of detections (1 002), with common duiker (*Sylvicapra grimmia*) having the second highest (939). Klipspringer (*Oreotragus oreotragus*)

**Table 3:** Model selection values for the top three ranked generalised linear models (with gamma error distribution and identity link function) with the effective number of species (ENS) as the response variable and the covariates: Longitude, Average Annual Precipitation, Livestock Relative Abundance (RAI), Terrain Ruggedness and Biome. Models were evaluated on their goodness of fit prior to ranking with AICc. Those with suboptimal fit were removed

| Model   | AICc    | ΔAICc |
|---|---------|-------|
| ENS = $\beta_0 + \beta_1$ Longitude                           | 104.581 |       |
| ENS = $\beta_0 + \beta_1$ Average Annual Precipitation        | 107.017 | 2.435 |
| ENS = $\beta_0 + \beta_1$ Longitude + $\beta_2$ Livestock.RAI | 107.032 | 0.015 |
| ENS = $\beta_0$   | 116.494 | 9.462 |
| ENS = $\beta_0 + \beta_1$ Terrain Ruggedness                  | 116.639 | 0.145 |
| ENS = $\beta_0 + \beta_1$ Latitude                            | 118.594 | 1.955 |
| ENS = $\beta_0 + \beta_1$ Livestock.RAI                       | 119.060 | 0.466 |
| ENS = $\beta_0 + \beta_1$ Biome                               | 123.643 | 4.583 |

was only detected twice, and ground squirrel (*Xerus inauris*) was only detected at one site. Steenbok (*Raphicerus campestris*) and common hare (*Lepus saxatilis* and *Lepus capensis*) were both recorded at all but two sites. Only four species of conservation concern were detected, namely Cape mountain zebra (*Equus zebra zebra*), grey rhebok (*Pelea capreolus*), black-footed cat (*Felis nigripes*) and southern mountain reedbuck (*Redunca fulvorufula fulvorufula*). Seven domestic species (Supplementary Table S1) were detected, with sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos taurus*) being the most common. NMDS ordinations (stress = 0.218) showed no evidence for strong or discrete clustering of sites based on their community composition, though sites in the Savanna and Grassland biomes appeared to form a loose cluster (Figure 3). Rather, there was a gradual change in mammalian community composition with longitude surface fitted to the ordination.

The most parsimonious GLM retained only longitude as a significant predictor of the ENS for the 25 sites with species diversity increasing along a west–east gradient



**Figure 2:** Estimator-based (solid line) species accumulation curves for all 25 sites, obtained with incidence-based coverage (ICE), Chao 2, first-order Jackknife 1, second-order jackknife (Jackknife 2) and bootstrap richness estimators. Shaded polygons indicate the 95% confidence intervals

( $z = 4.018$ ,  $p = 0.0005$ ) (Table 4, Figure 4). The next most parsimonious model, with AICc being 2.43 higher, retained only average annual precipitation as a significant positive predictor of the ENS.

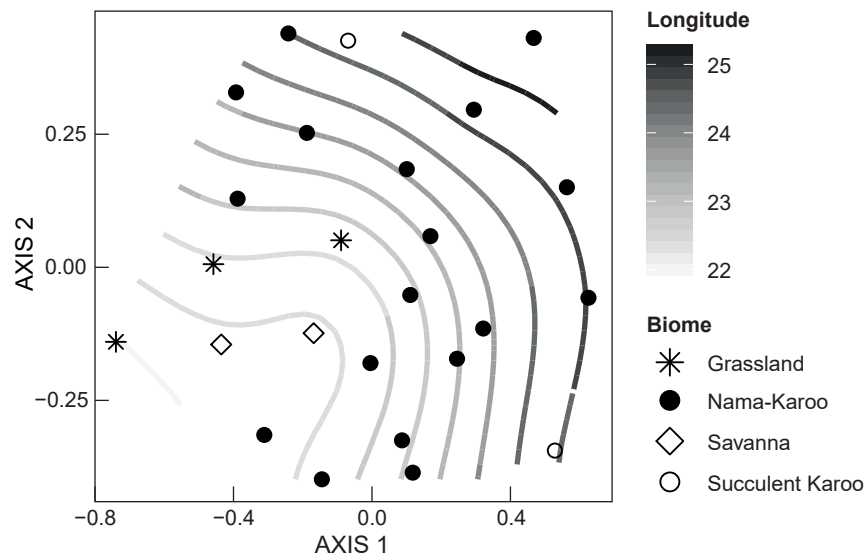
## Discussion

Understanding the pattern of species richness across a landscape may ultimately improve policy decisions at both the regional and local level (Hilty et al. 2012). The BioGaps project aims to provide such foundational biodiversity information within the existing SGEA (Todd et al. 2017). In doing so, areas of greatest biodiversity can be identified prior to exploration with the goal of mitigating or preventing the impacts of the proposed mining (Huston 1999; Hunter and Gibbs 2007; Hilty et al. 2012; Steenweg et al. 2017; Todd et al. 2017). This study contributed to the BioGaps project by illuminating the pattern of mammal species richness and diversity across the SGEA.

Our results reveal that the SGEA supports a minimum of 38 mammal species (>0.5 kg), most of which are classified as Least Concern ( $n = 34$ ) according to the latest Red List data (Table 2). As only a few of the species detected in this study were of conservation concern ( $n = 4$ ), this suggests that the assemblage of mammal species present within the SGEA is largely resilient to current anthropomorphic pressures. The common hare species were found at the majority of sites, along with steenbok, aardvark and greater kudu (Table 2). These adaptable species have large

ranges that extend far beyond the SGEA. These findings are similar to those of Mann et al. (2015) in the Little Karoo and Drouilly et al. (2018) in the Great Karoo, which reported a total of 36 and 33 species, respectively. Together these results suggest that while many of the species that historically occurred in the Karoo were not detected in this study, pastoralism in semi-arid rangelands currently support a cosmopolitan community of wildlife. It is important to note the need to add information on small mammals to the mammal taxa assessment for the BioGaps project.

In our study longitude emerged as the best predictor of the ENS, with the ENS increasing from west to east in the SGEA. Similarly, mammal species assemblages appear to be similar based on the longitudinal positioning of sites in the NMDS space (Figure 3). The scale of the study (25 sites across the 120 000 km<sup>2</sup>) meant that this broad predictor of diversity is more apparent than specific predictors such as NDVI. Longitudinal gradients effectively integrate a variety of environmental and climatic variables at the continental scale, and so provide a proxy for key drivers of biodiversity, such as rainfall, topography and temperature (Qian et al. 1998; Andrews et al. 2000; Kooyers et al. 2014). More productive areas in the east of South Africa are able to support more diverse mammal communities than their arid counterparts in the west (Andrews et al. 2000). Rainfall isohyets in the Karoo also reveal a clear pattern of increasing rainfall as one shifts from the Nama-Karoo biome to both Grassland and Savanna biomes in the east (Milton et al. 1997; Mucina and Rutherford 2006). These

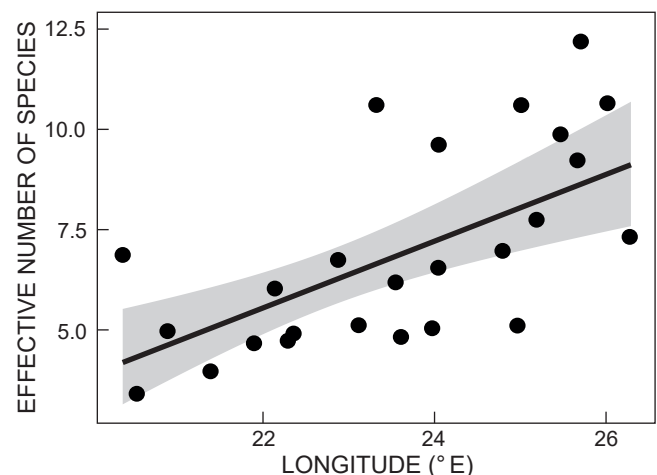


**Figure 3:** NMDS of occurrence based on Jaccard-index of similarity of all 25 sites, overlaid with a fitted longitude surface (grey contour lines) (Stress value: 0.218). The biomes of each site are indicated by distinct symbols.

more mesic biomes may increase overall biodiversity by supporting species not commonly found in the extensive Nama-Karoo biome. NMDS ordinations, whilst showing no distinct patterning, had very loose clustering of sites found within the Savanna ( $n = 2$ ) and Grassland ( $n = 3$ ) biomes (Figure 3). Visiting additional sites would most likely increase detections of novel species to these biomes, strengthening the clustering in the ordination space and the predictive power of longitude in the GLM.

Contrary to our predictions, none of the other variables (viz. average annual precipitation, NDVI, terrain roughness and livestock RAI) were significant predictors of the ENS. Average annual precipitation was the second-best predictor of the ENS variation in this study, and was positively correlated with both longitude and NDVI. NDVI was also positively correlated with longitude, and thus longitude may serve as a suitable proxy for productivity (which in turn influences mammal species richness and diversity) (Qian et al. 1998; Andrews et al. 2000). Terrain roughness was not a significant predictor of the ENS, which contrasts with other studies that have revealed an intrinsic link between species richness and ruggedness (Scott et al. 2001; Karanth et al. 2009; Nunn and Puga 2012). Few of our sites were characterised by rugged terrain with most being largely flat and interspersed with small hills called 'koppies' (Dean and Milton 1999). Thus species known to prefer more rugged and mountainous terrain, such as klipspringer, chacma baboon (*Papio ursinus*), leopard and rock hyrax (*Procavia capensis*), were seldom or not detected in our study.

Plant communities in this arid ecosystem have been shown to have limited natural recovery or rehabilitation potential and, consequently, persistent and extensive livestock grazing is thought to have irrevocably altered the carrying capacity of the arid landscape (Dean et al. 2003; Seymour et al. 2010). This may also explain why livestock RAI did not have a significant effect on the ENS in our analysis – the historical damage to the flora and hence fauna having resulted in a permanent shift in the baseline



**Figure 4:** Effect of longitude on the Effective Number of Species. Solid line and shaded areas are predictions and 95% confidence intervals from a GLM with a Gamma error distribution and identity link function (see Table 4)

**Table 4:** Summary statistics of most parsimonious GLM (AICc = 104.5814) for the effect of longitude on the effective number of species in the SGEA ( $n = 25$ )

| Variable  | Estimate | SE     | Z      | P      |
|-----------|----------|--------|--------|--------|
| Intercept | -12.2521 | 4.6292 | -2.647 | 0.0144 |
| Longitude | 0.8137   | 0.2025 | 4.018  | 0.0005 |

for many species. For example, black-backed jackals (*Canis mesomelas*) were detected at almost every site in our study despite widespread persecution and extensive jackal-proof fencing fragmenting the landscape. Clearly, the jackal has adapted to the new baseline of fences, hunters and abundant, easy-to-catch sheep (Nattrass and Conradie 2015; van der Weyde et al. 2018). Furthermore, many farmers manage and maintain medium to large antelope

present on their property, both as a source of food and supplementary income through sport and trophy hunting (Saayman et al. 2011). This may include replenishing breeding stock of naturally occurring antelope (e.g. greater kudu) or introducing a relatively novel species, such as impala. Interestingly, some of the farmers in this study managed their southern mountain reed buck (*Redunca fulvorufula fulvorufula*) for trophy hunting, despite the species being recently classified as Endangered due to an estimated population decline of 61%–73% across various protected areas (Child et al. 2016).

Rare species, including riverine rabbit, leopard and brown hyena (*Hyaena brunnea*), were not detected at any sites. Interestingly, these species only corresponded to the missing species predicted by the non-parametric richness estimator Jackknife2 (Figure 2). Chao, Jackknife1 and Bootstrap all predicted similar number of species as the observed value. Although we did optimise our camera trapping array to detect riverine rabbits at a local scale, their absolute rarity throughout their known distribution meant it was extremely unlikely that we would detect them. Consequently, for these species specialist reports (e.g. Ahlmann et al. 2000) and the relevant Red List data (Child et al. 2016) should be used to inform proposed development activities. Leopards and brown hyena do persist within the SGEA as confirmed by other scientific surveys (Collins and du Toit 2016), farmer observations, and observations by local conservation authorities (CapeNature quarterly reports). Leopards are typically confined to the rugged fold mountains that divide the Little and Great Karoo (Swanepoel et al. 2013) and, together with other large carnivores, were extirpated from most low-lying, flat land used for livestock farming (Boshoff et al. 2016; Nattrass et al. 2017). In this regard, Drouilly et al. (2018) found that brown hyena and leopard were absent from farmland but present in a nearby protected area.

Our results reveal no particular hotspots in mammal species diversity across the SGEA, with almost no species of conservation concern detected across the 25 intensively sampled sites. The best predictor of the ENS was longitudinal position, which integrates a variety of environmental and climatic variables and so provides a proxy for key drivers of biodiversity, such as rainfall and soil productivity across biomes. The species richness across all sites is comparable to other recent findings for mammals on farmland in semi-arid regions of the Karoo (Bösing et al. 2014; Mann et al. 2015; Drouilly et al. 2018). This suggests that the Karoo currently supports a diverse community of wildlife despite hundreds of years of sustained human impact, in the form of extensive livestock grazing with its itinerant fencing, lethal management of predators, road network and increasing human population (Dean and Milton 1999; Mann et al. 2015; Drouilly et al. 2018). Our study provides an important baseline for both the BioGaps project and government, allowing for management to make informed decisions and set regional limits of acceptable change linked to mining activities. This study's 25 (and preferably more) sites should be incorporated into a long-term monitoring program, aimed at systematically assessing the impact future land-use changes will have on species diversity and richness in the Karoo.

**Acknowledgements** — This work is based on research supported wholly/in part by the National Research Foundation of South Africa (Grant number 98864). Grant 98864 was awarded through the Foundational Biodiversity Information Programme (FBIP), a joint initiative of the Department of Science of Technology (DST), the National Research Foundation (NRF) and the South African National Biodiversity Institute (SANBI). In particular, we wish to thank Mrs Carol Poole and Mrs Gigi Laidler for proving logistical assistance during the study. We thank Dr H Robinson and N Robinson, who provided assistance processing the TRMM GIS layers. The Institute for Communities and Wildlife in Africa is gratefully acknowledged for donating field equipment, funding and providing logistical support for fieldwork. In addition, we wish to thank two anonymous reviewers for their insightful comments on the manuscript. Finally, we wish to thank the many Karoo farmers, who generously allowed us access to their farms.

## References

- Ahlmann V, Collins K, Seal US. 2000. Riverine rabbit (*Bunolagus monticularis*): a population and habitat viability assessment workshop. Final report. Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).
- Andrews P, O'Brien EM. 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology (London)* 251: 205–231.
- Aster GDEM. 2011. ASTER GDEM is a product of NASA and METI. Sioux Falls, SD: NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center.
- Bartoń K. 2018. MuMIn: multi-model inference. R package version 1.42.1. Available at <https://CRAN.R-project.org/package=MuMIn>.
- Beinart W. 2004. *The rise of conservation in South Africa: settlers, livestock, and the environment*. Oxford: Oxford University Press.
- Boshoff A, Landman M, Kerley G. 2016. Filling the gaps on the maps: historical distribution patterns of some larger mammals in part of southern Africa. *Transactions of the Royal Society of South Africa* 71: 23–87.
- Bösing BM, Haarmeyer DH, Dengler J, Ganzhorn JU, Schmiedel U. 2014. Effects of livestock grazing and habitat characteristics on small mammal communities in the Knersvlakte, South Africa. *Journal of Arid Environments* 104: 124–131.
- Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52: 675–685.
- Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT (eds). 2016. *The Red List of mammals of South Africa, Swaziland and Lesotho*. Pretoria: South African National Biodiversity Institute; Johannesburg: Endangered Wildlife Trust.
- Christenson DP, Goldfarb JL, Kriner DL. 2017. Costs, benefits, and the malleability of public support for "Fracking". *Energy Policy* 105: 407–417.
- Collins K, du Toit JT. 2016. Population status and distribution modelling of the critically endangered riverine rabbit (*Bunolagus monticularis*). *African Journal of Ecology* 54: 1–12.
- Colwell RK, Mao CX, Chang J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85: 2717–2727.
- Colyn RB, Radloff FGT, O'Riain MJ. 2018. Camera trapping mammals in the scrubland's of the Cape Floristic Kingdom—the importance of effort, spacing and trap placement. *Biodiversity and Conservation* 27: 503–520.
- Dean WRJ, Milton S. 1999. *The Karoo: ecological patterns and processes*. Cambridge: Cambridge University Press.
- Dean WRJ, Milton SJ, Hoffman MT, Cowling RM. 2003. Did the flora match the fauna? Acocks and historical changes in Karoo



- biota. *South African Journal of Botany* 69: 68–78.
- Didan K. 2015. MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006.
- Drouilly M, Clark A, O'Riain MJ. 2018. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: a case for dryland systems globally. *Biological Conservation* 224: 16–25.
- Duthie AG. 1989. The ecology of the riverine rabbit *Bunolagus monticularis*. PhD thesis, University of Pretoria, South Africa.
- du Toit JT, Cumming DHM. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8: 1643–1661.
- Ellis KS, Larsen RT, Whiting JC, Wilson TL, McMillan BR. 2017. Assessing indirect measures of abundance and distribution with remote cameras: simplifying indices of activity at pygmy rabbit burrows. *Ecological Indicators* 77: 23–30.
- Gillman LN, Wright SD. 2006. The influence of productivity on the species richness of plants: a critical assessment. *Ecology* 87: 1234–1243.
- Gotelli N, Colwell R. 2011. Estimating species richness. In: Magurran AE, McGill BJ (eds), *Biological diversity: frontiers in measurement and assessment*. Oxford: Oxford University Press. pp 39–54.
- Gould W. 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. *Ecological Applications* 10: 1861–1870.
- Hilty JA, Chester CC, Cross MS. 2012. *Climate and conservation: landscape and seascape science, planning and action*. Washington, DC: Island Press.
- Hoffman MT, Cowling RM. 1990. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo – fact or fiction? *South African Journal of Science* 86: 286–294.
- Hoffmann A, Zeller U. 2005. Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. *Belgian Journal of Zoology* 135: 91–96.
- Hofmeester TR, Rowcliffe JM, Jansen PA. 2017. A simple method for estimating the effective detection distance of camera traps. *Remote Sensing in Ecology and Conservation* 3: 81–89.
- Hughes GO, Thuiller W, Midgley GF, Collins K. 2008. Environmental change hastens the demise of the critically endangered riverine rabbit (*Bunolagus monticularis*). *Biological Conservation* 141: 23–34.
- Hunter ML, Gibbs JP. 2007. *Fundamentals of conservation biology*. Hoboken: John Wiley and Sons.
- Huston MA. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393–401.
- Jost L. 2006. Entropy and diversity. *Oikos* 1137: 363–375.
- Karanth KK, Nichols JD, Hines JE, Karanth KU, Christensen NL. 2009. Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology* 46: 1189–1200.
- Kinnaird MF, O'Brien TG. 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. *Conservation Biology* 26: 1026–1039.
- Kooyers NJ, Gage LR, Al-Lozi A, Olsen KM. 2014. Aridity shapes cyanogenesis cline evolution in white clover (*Trifolium repens* L.). *Molecular Ecology* 23: 1053–1070.
- Lagesse JV, Thondhlana G. 2016. The effect of land-use on small mammal diversity inside and outside the Great Fish River Nature Reserve, Eastern Cape, South Africa. *Journal of Arid Environments* 130: 76–83.
- Laurance WF, Sayer J, Cassman KG. 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution* 29: 107–116.
- Lite SJ, Bagstad KJ, Stromberg JC. 2005. Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *Journal of Arid Environments* 63: 785–813.
- Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, Scott EM, Smith RI, Somerfield PJ, Watt AD. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology and Evolution* 25: 574–582.
- Mann GKH, Lagesse JV, O'Riain MJ, Parker DM. 2015. Beefing up species richness? The effect of land-use on mammal diversity in an arid biodiversity hotspot. *African Journal of Wildlife Research* 45: 321–331.
- Mannion PD, Upchurch P, Benson RBJ, Goswami A. 2014. The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution* 29: 42–50.
- Mayer A. 2016. Risk and benefits in a fracking boom: evidence from Colorado. *Extractive Industries and Society* 3: 744–753.
- Meng Q. 2017. The impacts of fracking on the environment: a total environmental study paradigm. *Science of the Total Environment* 580: 953–957.
- Milton SJ, Yeaton RI, Dean WRJ, Vlok JHJ. 1997. Succulent Karoo. In: Cowling RM, Richardson DM, Pierce SM (eds), *Vegetation of southern Africa*. Cambridge: Cambridge University Press. pp 131–166.
- Minasny B, McBratney AB. 2006. A conditioned Latin hypercube method for sampling in the presence of ancillary information. *Computers and Geosciences* 32: 1378–1388.
- Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Mucina L, Rutherford MC (eds). 2006. *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia* 19. Pretoria: South African National Biodiversity Institute.
- Natrass N, Conradie B. 2015. Jackal narratives: predator control and contested ecologies in the Karoo, South Africa. *Journal of Southern African Studies* 41: 1–19.
- Natrass N, Conradie B, Drouilly M, O'Riain MJ. 2017. *A brief history of predators, sheep farmers and government in the Western Cape, South Africa*. Working Paper 398. Cape Town: Centre for Social Science Research, University of Cape Town.
- Nunn N, Puga D. 2012. Ruggedness: the blessing of bad geography in Africa. *Review of Economics and Statistics* 94: 20–36.
- O'Brien TG, Baillie JEM, Krueger L, Cuke M. 2010. The wildlife picture index: monitoring top trophic levels. *Animal Conservation* 13: 335–343.
- Okes NC, O'Riain MJ. 2017. Otter occupancy in the Cape Peninsula: estimating the probability of river habitat use by Cape clawless otters, *Aonyx capensis*, across a gradient of human influence. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27: 706–716.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens M, Wagner H. 2018. Vegan: community ecology package. R package version 2.5-2. Available at <https://CRAN.R-project.org/package=vegan>.
- QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- Qian H, Klinka K, Kayahara GJ. 1998. Longitudinal patterns of plant diversity in the North American boreal forest. *Plant Ecology* 138: 161–178.
- R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Roudier P. 2018. clhs: a R package for conditioned Latin

- hypercube sampling. R package version 0.7-0. Available at <https://CRAN.R-project.org/package=clhs>.
- Rouget M, Richardson DM, Cowling RM, Lloyd JW, Lombard AT. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112: 63–85.
- Roux PW, Vorster M, Zeeman PJL, Wentzel D. 1981. Stock production in the Karoo region. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* 16: 29–35.
- Saayman M, van der Merwe P, Rossouw R. 2011. The impact of hunting for biltong purposes on the SA economy. *Acta Commercii* 11: 1–12.
- Scholes RJ, Dowty PR, Caylor K, Parsons DAB, Frost PGH, Shugart HH. 2002. Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science* 13: 419–428.
- Scholes R, Lochner P, Schreiner G, Snyman-Van der Walt L, de Jager M (eds). 2016. *Shale gas development in the central Karoo: a scientific assessment of the positive and negative consequences*. Report no. CSIR/02100/EMS/ER/2016/15241/B. Pretoria: CSIR.
- Schreiner GO, Snyman-Van der Walt L. 2017. Modelling social-ecological risks of shale gas development in the central Karoo. *International Journal of Sustainable Development and Planning* 13: 20–23.
- Scotchman IC. 2016. Shale gas and fracking: exploration for unconventional hydrocarbons. *Proceedings of the Geologists' Association* 127: 535–551.
- Scott JM, Davis FW, McGhie RG, Wright RG, Groves C, Estes J. 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications* 11: 999–1007.
- Seymour CL, Dean WRJ. 1999. Effects of heavy grazing on invertebrate assemblages in the Succulent Karoo, South Africa. *Journal of Arid Environments* 43: 267–286.
- Seymour CL, Milton SJ, Joseph GS, Dean WRJ, Dithobolo T, Cumming GS. 2010. Twenty years of rest returns grazing potential, but not palatable plant diversity, to Karoo rangeland, South Africa. *Journal of Applied Ecology* 47: 859–867.
- Shannon CE. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27: 379–423.
- Sollmann R, Mohamed A, Samejima H, Wilting A. 2013. Risky business or simple solution – relative abundance indices from camera-trapping. *Biological Conservation* 159: 405–412.
- Steenweg R, Hebblewhite M, Kays R, Ahumada J, Fisher JT, Burton C, Townsend SE, Carbone C, Rowcliffe JM, Whittington J, Brodie J, Royle JA, Switalski A, Clevenger AP, Heim N, Rich LN. 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment* 15: 26–34.
- Swanepoel LH, Lindsey P, Somers MJ, van Hoven W, Dalerum F. 2013. Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation* 16: 41–50.
- Takayabu N, Shige S. 2011. TRMM 3H25 - Monthly Spectral Latent Heating.
- Tobler MW. 2007. Camera base version 1.3. Fort Worth: Botanical Research Institute of Texas.
- Tobler MW, Carrillo-Percegue SE, Pitman RL, Mares R, Powell G. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation* 11: 169–178.
- Todd SW. 2006. Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. *Journal of Applied Ecology* 43: 293–304.
- Todd SW, Hoffman T, Henschel JR, Cardoso AW, Brooks M, Underhill LG. 2017. The potential impacts of fracking on biodiversity of the karoo basin, South Africa. In: Glazewski J, Esterhuysen S (eds), *Hydraulic fracturing in the Karoo: critical legal and environmental perspectives*. Cape Town: Juta. pp 278–301.
- Tuomisto H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* 164: 853–860.
- Vermeulen PD. 2012. A South African perspective on shale gas hydraulic fracturing. Paper presented at the International Mine Water Association, Annual Conference, Bunbury, Australia, 29 September–4 October 2012.
- Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30: 257–300.
- van der Weyde LK, Mbisana C, Klein R. 2018. Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. *Biological Conservation* 220: 21–28.
- Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34: 273–309.
- Woese C, Kandler O, Wheelis M. 1990. Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences of the USA* 87: 4576–4579.
- World Bank. 2014. *World development indicators 2014*. Washington, DC: World Bank Publications.
- Yan H, Liang C, Li Z, Liu Z, Miao B, He C, Sheng L. 2015. Impact of precipitation patterns on biomass and species richness of annuals in a dry steppe. *PLoS ONE* 10: e0125300.