

Original article

The impacts of past cultivation on the reptiles in a South African grassland

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Abstract.—Habitat transformation is the primary anthropogenic threat to global biodiversity. Fragmentation of reptile populations following habitat transformation within a landscape can lead to the extirpation of species. We investigated the effects of land-use on the species richness and abundance of reptile assemblages in three habitat types (two natural and one modified) in the grasslands of Gauteng, South Africa. Using trap arrays, we surveyed reptiles in primary grassland with little or no rock cover, primary grassland with large quartzite outcrops and scattered rocks, and secondary grasslands that were historically ploughed and cropped. We measured vegetation height and vegetation cover at these same localities. We caught significantly fewer reptile species in the historically cultivated sites than in either of the two natural habitat types. Differences in the reptile assemblage of each habitat type were not explained by either the spatial location or the vegetation structure of our trap sites but were well explained by the sites' habitat type. Estimates of total species richness indicated that we were able to adequately sample the reptile assemblages in the three habitat types, further supporting our observation of reduced species richness in the secondary grasslands. We infer that habitat transformation associated with cultivation e.g., rock removal, has had a detectable, negative impact on the species richness and composition of the local reptile assemblages. We recommend that land-use planning in Gauteng emphasise the need for areas of inter-connected, untransformed habitat in order to mitigate the negative impacts of habitat transformation on the local reptile diversity.

Key words.—Reptile, species richness, grassland, cultivation, sample-based rarefaction.

The loss or degradation of natural habitat and ecosystems is the single biggest cause of biodiversity loss in South Africa's terrestrial ecosystems (Driver *et al.* 2005). Driver *et al.* (2005) quantified the spatial location and severity of threats to the country's biodiversity but did not assess the potential impacts of land-use change on each of the components of biodiversity. The impacts of land-use change and habitat modification/degradation on the reptiles of South Africa are currently poorly described (Smart *et al.* 2005; Masterson *et al.* 2008), despite evidence suggesting that reptiles are particularly sensitive to land-use (e.g. Santelmann *et al.* 2006). Research into the impacts of land-use change is particularly cru-

cial in areas where human activities are densely concentrated, e.g. Gauteng, South Africa.

Gauteng occupies only 1.4 % (17 010 km²) of South Africa's land area but is home to 21.5 % (10.4 million) of its estimated 48 million people (Statistics South Africa 2008) and produces 33.9 % of South Africa's Gross Domestic Product (GDP; Department of Environmental Affairs and Tourism 2005). Between 2001 and 2008, the population density of the province rose from 520 people per km² (Department of Environmental Affairs and Tourism 2005) to 616 people per km² (Statistics South Africa 2008). This rapid human population growth is placing increasing pressure on the natural envi-

ronment in Gauteng. In addition to the land allocated to meet the housing and infrastructural needs of the population, large areas of the province's sweet grasslands have been cleared to produce maize and other agricultural products (Department of Environmental Affairs and Tourism 2005). The present rate of habitat transformation shows no sign of declining in the short or medium-term, which emphasises the need for conservation authorities to identify the impacts of continuing transformation on biodiversity and develop plans to mitigate them.

Responses of reptiles to habitat modification have been linked to numerous factors that include the type of disturbance involved (Jones *et al.* 2000); changes in microhabitat availability (James & M'Closeky 2003; Goode *et al.* 2005); changes in the rates of predation following modification (Reinert 1993); changes in the thermal properties of the habitat (Lillywhite 1987) and intrinsic characteristics such as the species' dispersal and recolonisation abilities (Twigg & Fox 1991). Due to their limited mobility, reptiles are susceptible to habitat fragmentation and transformation (Webb & Shine 1997). Continued habitat transformation and fragmentation of reptile populations within a landscape can lead to extirpation, but the responses of particular species to habitat modification are not easily predicted and often require explicit testing or monitoring.

Gauteng lies at the interface between the Savanna and Grassland biomes of South Africa. Grasslands in South Africa are under extreme pressure and formally protected areas account for only 2 % of the biome's total area (Bredenkamp 2002). Threats to the Grassland biome include: (1) high agricultural potential, (2) high mining potential, (3) habitat fragmentation and (4) the high suitability for the invasion of alien plant species (Driver *et al.* 2005). Consequently, the Grassland biome has the highest proportion of threatened ecosystems

(around 60 %; Driver *et al.* 2005) of all the nine recognised biomes in South Africa. Several grassland-specialist reptile species are declining in abundance and Area of Occupancy e.g., *Chamaesaura anguina anguina* and *Chamaesaura aenea* as well as *Homoroselaps dorsalis* (see M. Bates, unpubl.; Branch 1988). To date, the presence of the two *Chamaesaura* species has not been confirmed in any of the six provincially protected areas of Gauteng, while *H. dorsalis* is known only from Suikerbosrand Nature Reserve (Whittington-Jones *et al.* 2008). Despite numerous surveys throughout Gauteng, only four specimens of the three species - two of *C. aenea* and two of *H. dorsalis* (see Whittington-Jones *et al.* 2008; D. Koen, unpubl. data) - have been collected since 2000. The rarity of these species coupled with the rapid increase in human population density in the province suggests that the pressure on these grassland species is increasing.

Recognising the pressure on the natural environment and the links between reptile diversity and habitat structure (Mushinsky 1985; Block *et al.* 1998; Cavitt 2000; Woinarski & Ash 2002; Read 2002; James 2003; Maritz and Alexander 2007; Masterson *et al.* 2008), we investigated the effects of land-use and habitat type on the species richness and abundance of reptile assemblages in three habitat types (two natural and one modified) in the grasslands of Gauteng, South Africa. The primary aim of our investigation was to assess the impacts of historical cultivation on the local reptile assemblages in these threatened grasslands.

MATERIALS AND METHODS

Study Site and Reptile Survey.—Suikerbosrand Nature Reserve (26° 30' S; 28° 15' E) is located approximately 40 km south of Johannesburg, Gauteng Province, South Africa, and incorporates the major portion of the Suikerbosrand, a high lying plateau named for

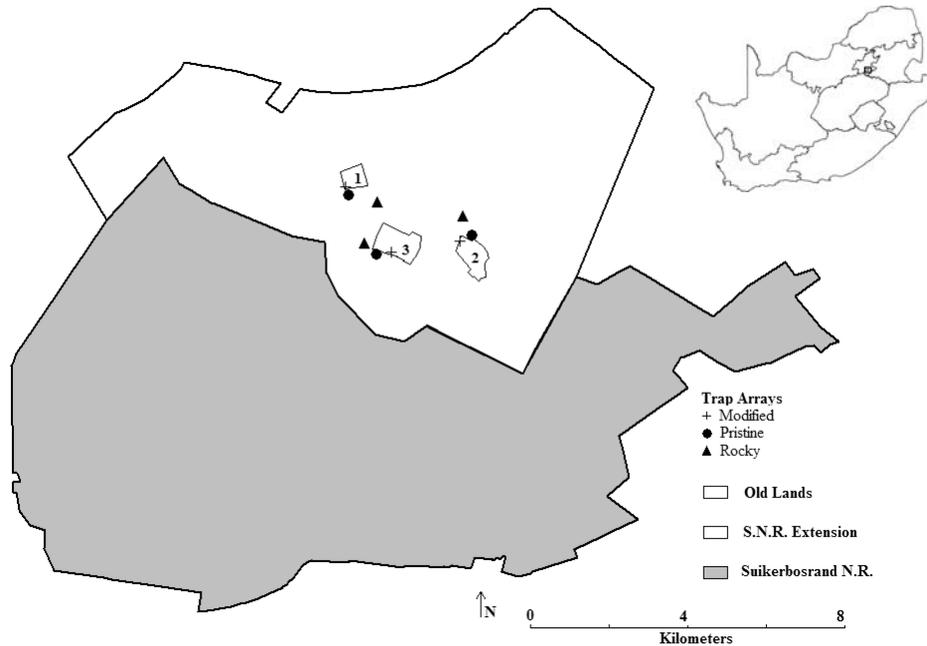


Figure 1. A map of the study site, the positions of the nine trap arrays in relation to each other and the three historically cultivated areas (numbered polygons) sampled. The location of Suikerbosrand Nature Reserve in Gauteng, South Africa is shown (inset).

the abundant Highveld Protea (*Protea caffra*). Originally proclaimed in 1973, Suikerbosrand Nature Reserve was enlarged by the purchase of 6 936 ha of adjacent mixed agricultural lands in 2005. As a result of the acquisition, Suikerbosrand Nature Reserve encompasses 18 587 ha and is the largest grassland reserve in Gauteng. Altitude on the reserve ranges from 1 545 to 1 917 m a.s.l. Rainfall is highly seasonal, with most of the annual mean of 675 mm falling in summer, between October and March (Shultze 1997). Vegetation on the recently-acquired extension is classified as Tsakane Clay Grassland (Mucina & Rutherford 2005). Tsakane Clay Grassland is a highly threatened vegetation type with 63 % of the vegetation type irreversibly transformed (Mucina & Rutherford 2006).

We surveyed reptiles on the extension of Suikerbosrand Nature Reserve between 1 December 2005 and 20 April 2006 using trap arrays. Nine trap arrays were installed in three habitat types i.e., three clusters of sites (Fig. 1). Trap clusters were situated $1\,976 \pm 550$ m from each other (min = 1 398 m; max = 2 495 m), while trap arrays within clusters were 518 ± 204 m apart (min = 223 m; max = 830 m). Habitat types in each cluster were (1) primary grassland with little or no rock cover (pristine sites), (2) primary grassland with large quartzite outcrops and scattered rocks (rocky sites) and (3) secondary grasslands that were historically ploughed, cultivated and cropped (modified sites). Trap arrays in the modified habitats were placed between 50 to 100 m from the habitat edge. The layout of the trap arrays used in this field survey has been described

elsewhere (Maritz *et al.* 2007). In short, each array consisted of 36 m of plastic drift fence, five pitfall traps and eight mesh funnel traps installed in a closed-cross configuration. Traps were checked daily and all captured reptiles were identified to species level and released at the site of capture. Lizard species were marked using a trap-specific toe-clip code to allow us to identify dispersal events between trap arrays. Snake species were not marked. Nomenclature is from Branch (1998), although we use the generic assignment of *Trachylepis* Fitzinger 1843 instead of *Mabuya* Fitzinger 1826 (see Bauer 2003).

The disturbance histories of the three cultivated areas differ from each other and the surrounding grassland. Cultivated area 1 was ploughed in 2005 just prior to our survey in order to allow for the re-seeding of indigenous species at the site. Cultivated area 2 has not been ploughed since at least 2002 and possibly even 2000, while sunflowers were last planted on cultivated area 3 during the 2002/2003 growing season. Unfortunately, accurate fire records for the extension exist only from 2004 onwards when the area was included in Suikerbosrand Nature Reserve, but it is likely that fire frequency in the cultivated areas was reduced by the pre-spring ploughing and seeding. The majority of natural fires at Suikerbosrand Nature Reserve are started by lightning during the early spring rains in September and October.

Vegetation Measures.—We measured two structural characteristics of the vegetation within 400 m² of each trap array using a grid of 20 quadrats (size = 1 m²; as per Masterson *et al.*, 2008). Vegetation height was measured at each of the four corners of each quadrat; vegetation cover was estimated as the proportion of soil obscured from view by the vegetation within the quadrat. Mean vegetation height and mean vegetation cover were calculated for each trap array. Measures of vegetation cover (percent-

ages) were arcsine transformed prior to data analysis.

Data Analysis.—We compared the mean species richness and mean number of reptiles captured in each habitat type and each cluster using one-way Analysis of Variance (ANOVA). We used General Linear Modelling (GLM) to test the significance and compare the explanatory power of (1) habitat type, (2) cluster, (3) mean vegetation height, (4) mean vegetation cover and (5) the total number of reptiles captured on the observed species richness (S_{obs}) at each trap array. Factors with a significant effect on the total number of species recorded at each site were then combined using forward selection to test the significance of their interactions. We also compared the relative species richness i.e., species richness per number of individuals captured, and species density i.e., species richness per sample, of each habitat type and cluster using sample-based rarefaction (Gotelli & Colwell 2001). Sample-based rarefaction curves were produced using EstimateS version 7.5 (Colwell 2005) with a sample defined as the number of reptiles captured per group of traps i.e., habitat type or cluster, per day (N = 141 samples).

There is some disagreement as to the specific method by which confidence intervals should be used to confirm differences between rarefaction curves. Colwell *et al.* (2004) tested for the overlap of confidence intervals in their comparison of old growth and secondary growth forests. In contrast, Magurran (2004) analysed only the position of the mean value of the smaller rarefaction curve relative to the confidence interval of the larger curve in her comparison of *Drosophila* species richness between two surveys. The choice of method is strongly influenced by whether or not the two assemblages being compared can be assumed to be equivalent in their species composition. If the two assemblages can be assumed or are known to be equivalent, then the exclusion of the mean of the

Table 1. A summary of the total number of individual reptiles captured per habitat type and per species between December 2005 and April 2006. Recaptures of the toe-clipped lizard species are shown in brackets.

Family	Species	Number captured	Habitat type		
			Modified	Pristine	Rocky
Lizards					
Agamidae	<i>Agama aculeata distanti</i>	9 (2)	2	7 (2)	-
Cordylidae	<i>Cordylus vittifer</i>	4 (0)	-	1	3
Gerrhosauridae	<i>Gerrhosaurus flavigularis</i>	116 (40)	7	64 (30)	45 (10)
Lacertidae	<i>Nucras lalandii</i>	4 (1)	-	4 (1)	-
Scincidae	<i>Panaspis walbergii</i>	33	2	6	25
	<i>Trachylepis capensis</i>	130 (20)	59 (8)	50 (9)	21 (3)
	<i>Trachylepis varia</i>	26 (1)	3	5 (1)	18
Gekkonidae	<i>Pachydactylus capensis</i>	2	-	2	-
Snakes					
Typhlopidae	<i>Typhlops bibronii</i>	1	-	-	1
Atractaspididae	<i>Aparallactus capensis</i>	5	-	3	2
	<i>Atractaspis bibronii</i>	1	-	-	1
Colubridae	<i>Crotaphopeltis hotamboeia</i>	1	-	-	1
	<i>Dasypeltis scabra</i>	17	4	8	5
	<i>Lamprophis aurora</i>	4	1	1	2
	<i>Lamprophis capensis</i>	2	-	2	-
	<i>Lycophidion capense</i>	20	1	8	11
	<i>Psammophis crucifer</i>	17	2	9	6
	<i>Psammophylax rhombeatus</i>	13	2	10	1
	<i>Pseudaspis cana</i>	3	-	2	1
Elapidae	<i>Hemachatus haemachatus</i>	8	3	2	3
Viperidae	<i>Causus rhombeatus</i>	15	3	4	8
	<i>Bitis arietans arietans</i>	12	-	8	4
All species		443 (64)	89 (8)	196 (43)	158 (13)

smaller curve from the confidence interval of the larger curve is sufficient evidence of a significant difference in the species richness of the two assemblages. If two assemblages are assumed to be different in their species composition then the more conservative test, using the overlap of the confidence intervals, is most appropriate.

With no historical data on community composition available to us, we assumed that the reptile assemblages varied between the three habitat types and used the more conservative test in habitat comparisons. Consequently, we used the non-overlap of the confidence intervals at the largest sample size of the shorter rarefac-

tion curve to identify significant differences between two curves. We also formally tested our assumption regarding the variation in reptile assemblages by comparing the similarity of the reptile assemblages recorded in each of the three habitat types and clusters using the Analysis of Similarity (ANOSIM) sub-routine in Primer 5 (Clarke & Gorley 2001). Due to the right skew in the capture counts of the different species at each site, we log-transformed our data before calculating the Bray-Curtis Similarity between each pair of sites. Although skewness was not completely removed by this transformation it was greatly reduced.

Lastly, we evaluated the 'completeness' of our reptile sampling. In a sampling context, completeness is evaluated as the percentage of species estimated to occur in the sampling uni-

verse that were observed during sampling (Sobéron *et al.* 2007). Estimates of species richness for the three habitat types were generated using the nonparametric Chao1 and Chao2 species richness estimators (Chao 1984; Colwell 2005). The equations for the two estimators are functionally equivalent, but Chao1 uses abundance frequencies i.e. the number of individuals of each species captured, while Chao2 uses incidence frequencies i.e., the number of samples in which each species is observed. The terms 'singleton' and 'doubleton' refer to species that are represented by only one or two individuals in the total sample respectively, while the terms 'unique' and 'duplicate' refer to species that are observed in only one or two samples respectively. The estimators use the ratio of singletons to doubletons or uniques to duplicates to estimate the number of species

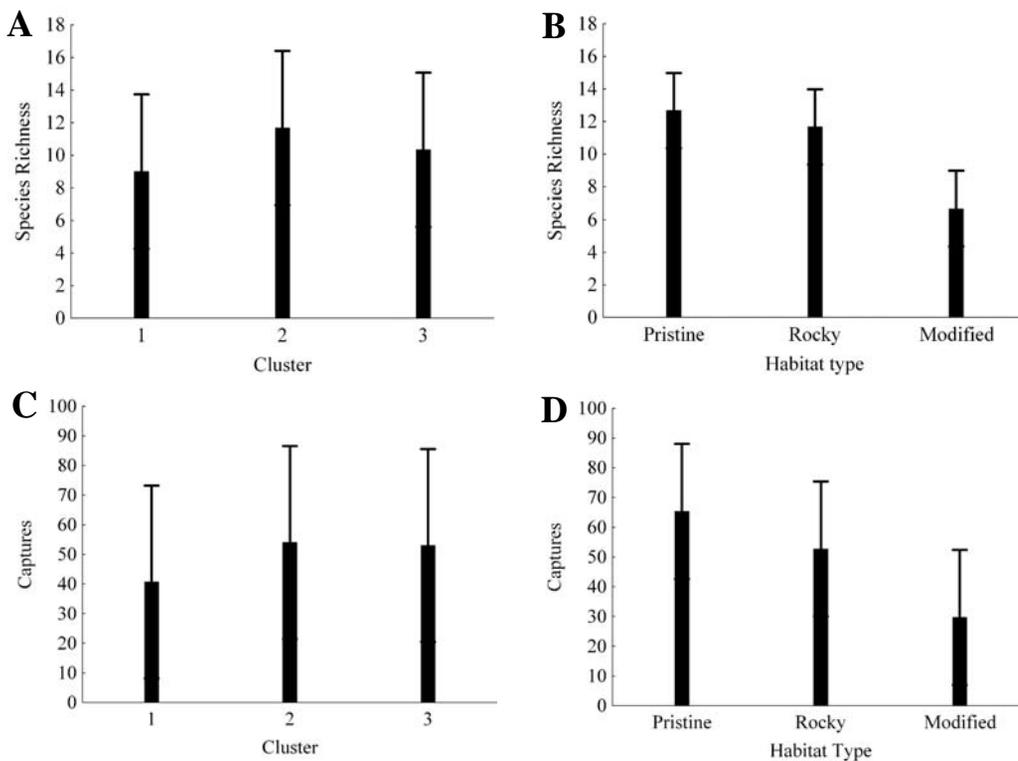


Figure 2. Mean reptile species richness for each cluster (A), and in each habitat (B), and mean number of reptile captures for each cluster (C) and each habitat (D), from trap array surveys in a South African grassland. Error bars indicate 95 % confidence limits.

Table 2. Observed (S_{obs}) and estimated species richness, with 95 % confidence intervals, for each of the three habitat types at two sample sizes (n). N refers to the total number of individuals captured in each habitat type during the sampling and is shown in Table 1 for each habitat type.

Habitat Type	$S_{\text{obs}} \pm 1 \text{ SD}$	S_{Chao1}	95 % CI		S_{Chao2}	95 % CI	
		Mean	Lower	Upper	Mean	Lower	Upper
n = N individuals							
Pristine	19 ± 0.70	19.20	19.01	23.06	19.20	19.01	23.04
Rocky	18 ± 2.15	21.33	18.54	38.47	21.31	18.54	38.34
Modified	12 ± 0.62	12.20	12.01	16.06	12.17	12.01	15.56
n = 89 individuals							
Pristine	16.16 ± 0.97	18.94	16.70	32.26	18.92	16.70	31.90
Rocky	15.24 ± 1.98	19.63	16.16	38.35	19.25	16.07	36.66
Modified	12.00 ± 0.62	12.20	12.01	16.06	12.17	12.01	15.56

that were not detected during the sampling.

We calculated two estimates of total species richness for the three habitat types using EstimateS (Colwell 2005). The first estimate was calculated using the maximum sample sizes available for each habitat type i.e., individuals captured and samples taken, while the second estimate was calculated when the number of individuals captured in the pristine and rocky habitat types equalled that of the total number captured in the modified habitat.

RESULTS

During the four months of trapping, we captured 443 reptiles comprising 8 lizard and 14 snake species (see Table 1 for details). Ten of the 22 species we captured were not captured in the modified habitat. Three species of snake, *Crotaphopeltis hotamboeia*, *Atractaspis bibronii* and *Typhlops bibronii*, were captured only once during the survey and only in the rocky habitat. Two species of lizard, *Nucras lalandii* and *Pachydactylus capensis*, were recorded on multiple occasions from only a single habitat type, i.e. pristine sites. Eight species (four snake and four lizard species) were captured twice or more in all three habitat types: *Causus rhombeatus*, *Dasypeltis scabra*, *Hemachatus haemachatus* and *Psammophis*

crucifer, *Gerrhosaurus flavigularis*, *Panaspis walbergii*, *Trachylepis capensis* and *Trachylepis varia*. *Trachylepis capensis* was the most frequently captured species at sites in the modified habitat, while *G. flavigularis* was the most frequently captured species at pristine sites.

Sixty-four lizards were recaptured during the survey (Table 1). Forty-three of the recaptures (67.2 %) were recorded at pristine sites, 13 (20.3 %) were recorded at rocky sites and eight (12.5 %) were recorded at modified sites (Table 1). *Gerrhosaurus flavigularis* was the most frequently recaptured species during the survey period, but *T. capensis* was the only species that was recaptured in all three habitat types and the only species to be recaptured at modified sites (Table 1). There was no indication of dispersal between trap arrays during the survey as all lizards were recaptured at the site of their initial capture.

There was no significant difference in the total number of species recorded at each of the three clusters (ANOVA: $F_{2,6} = 0.47$; $P = 0.64$; Fig. 2A) but significantly fewer species were captured at modified sites than at the pristine or rocky sites (ANOVA: $F_{2,6} = 11.63$; $P = 0.009$; Tukey HSD Post-hoc: *Pristine vs. Rocky*, $P = 0.74$; *Pristine vs. Modified*, $P = 0.01$; *Rocky vs. Modified*, $P = 0.02$; Fig. 2B). We found no sig-

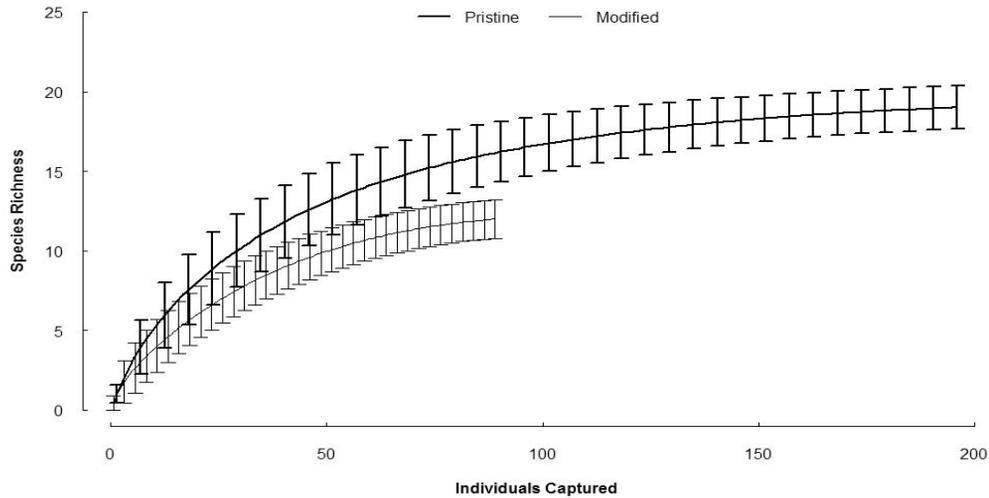
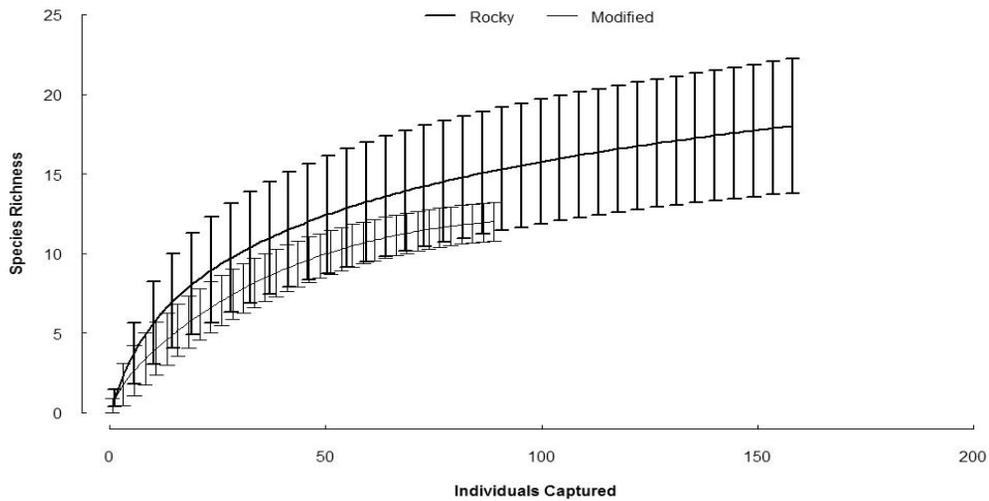
A**B**

Figure 3. Species richness per number of individuals for the pristine and modified habitat types (A) and rocky and modified habitat types (B) sampled between December 2005 and April 2006. Error bars indicate the 95 % confidence intervals for each curve, calculated by EstimateS version 7.5 (Colwell 2005). Statistically significant differences between the curves were determined by the non-overlap of confidence intervals at the point of comparison.

nificant difference in the total number of reptiles captured at sites in each cluster (ANOVA: $F_{2,6} = 0.31$; $P = 0.74$; Fig. 2C) or each habitat type (ANOVA: $F_{2,6} = 3.79$; $P = 0.09$; Fig. 2D).

Results of our sample-based rarefaction analysis were similar but not identical to the results of our ANOVA. As with the ANOVA, differences in reptile species richness of the three

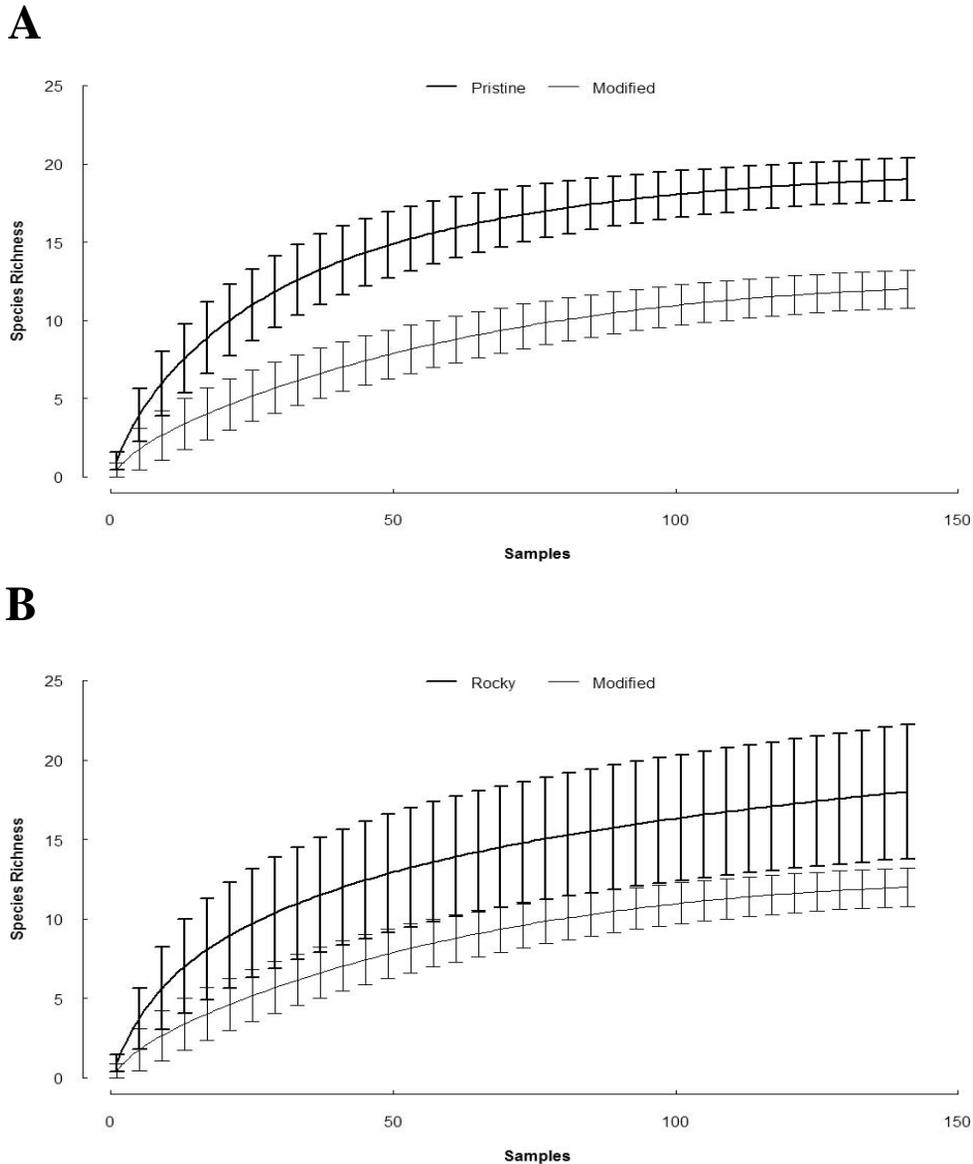


Figure 4. Species richness per number of samples for the pristine and modified habitat types (A) and rocky and modified habitat types (B) sampled between December 2005 and April 2006. Error bars indicate the 95 % confidence intervals for each curve, calculated by EstimateS version 7.5 (Colwell 2005). Statistically significant differences between the curves were determined by the non-overlap of confidence intervals at the point of comparison.

clusters were not significant, while pristine sites had significantly greater species richness than modified sites (Fig. 3A). More reptile species were captured at rocky sites than at

modified sites, but unlike the result of the ANOVA, the difference was not statistically significant due to confidence interval overlap (Fig. 3B). Modified sites had both the lowest

observed species richness and the narrowest 95 % confidence interval of the three habitat types ($S_{\text{obs}} \pm 1.96 \text{ SD} = 12 \pm 1.11$ species). Species density, the number of species recorded per sample, at the modified sites was significantly lower than the species density of both the pristine (Fig. 4A) and the rocky sites (Fig. 4B). Rocky sites showed the greatest heterogeneity in sample richness, as seen by the width of the confidence interval for rocky sites ($S_{\text{obs}} \pm 1.96 \text{ SD} = 18 \pm 6.09$ species). Species density varied insignificantly between the three clusters of trap arrays.

Species richness was well explained by habitat type (GLM: $F_{(2,6)} = 11.62$, $P = 0.009$, $R^2 = 0.79$) and the total number of reptiles captured (GLM: $F_{(1,7)} = 18.94$, $P = 0.003$, $R^2 = 0.73$) yet the bivariate model including habitat type and the total number of captures indicated a non-significant effect of the total number of captures on the observed species richness. Mean vegetation cover, mean vegetation height and cluster had no significant effect on the observed species richness recorded at each site (GLM: $P > 0.05$ in all univariate models).

The species composition of reptile assemblages varied by habitat type (ANOSIM: Global $R = 0.325$, $N_{\text{permutations}} = 280$, $P = 0.075$), but not by cluster (ANOSIM: Global $R = -0.029$, $N_{\text{permutations}} = 280$, $P = 0.53$). Pairwise comparisons of species similarity indicated a strong difference in the species composition of the modified and the rocky habitats (ANOSIM: $R = 0.67$, $N_{\text{permutations}} = 10$, $P = 0.10$) but little difference between the modified and pristine habitats (ANOSIM: $R = 0.33$, $N_{\text{permutations}} = 10$, $P = 0.30$). Although $P > 0.05$ in the modified-rocky pairwise comparison, the grouping of sites by habitat type produced as close a probability to 0.05 as could be achieved given the number of available permutations i.e., only one of the 10 permutations of R^* was greater than R . Trap sites in the pristine and rocky habitats were the

least different in species composition and abundance (ANOSIM: $R = -0.11$, $N_{\text{permutations}} = 10$, $P = 0.60$).

Estimates of species richness for each of the three habitat types are shown in Table 2. The 95 % confidence interval for the total estimated species richness in the modified habitat ranged from 12 to 16 species (Table 2), suggesting that the sampling of the species found in the modified habitat was between 75 and 100 % complete (mean = 98.36 %). At the equivalent level of sampling effort i.e., 89 individuals, the confidence intervals of the estimated species richness in the pristine and rocky habitats ranged from 17 to 32 species and 16 to 38 species respectively, suggesting the presence of nearly twice as many species as had been observed up to that point in both habitats (Table 2). With the inclusion of additional individuals, the upper bound of the confidence intervals for the pristine habitat decreased to 23 species, but remained at 38 species for the rocky habitat (Table 2). Consequently, the estimated sample completeness for the pristine habitat ranges from 83 and 100 % (mean = 98.96 %), while the sample completeness of the rocky habitat ranges from 47 and 100 % (mean = 84.39 %).

DISCUSSION

The results of our two analyses indicate that modified, secondary grassland in historically cultivated areas supports fewer species than the equivalent primary grassland. Differences in species richness were not significantly influenced by the spatial location of each site cluster or the structure of the vegetation in and around each trap array. As with species richness, we found no evidence for an effect of cluster on species composition. Our results indicate that habitat transformation via land-use change has had a detectable, negative impact on the species richness of the local reptile assemblages in the extension of

Suikerbosrand Nature Reserve. Estimates of species richness indicated that both the pristine and modified habitats were thoroughly sampled during our survey, while rocky habitat was satisfactorily, yet not as thoroughly, sampled. We also note that our results may even be considered a conservative assessment of the impacts of habitat transformation, given that our trap arrays were close to the edges of the modified habitat and may have been affected by edge effects.

Reptile assemblages are known to vary as the land-use of an area varies (Castellano & Valone 2006; Santelmann *et al.* 2006). Land-use change leads to changes in vegetation cover, which can influence other ecological factors such as predation rates (Castellano & Valone 2006). Santelmann *et al.* (2006) used weighted habitat associations to model the impacts of future agricultural land-use scenarios on the wildlife in Iowa, USA. They found that suitable habitat for reptile species was most negatively affected by a scenario in which the landscape was zoned for profitable agricultural production. Santelmann *et al.* (2006) also found that the response of reptiles to the future land-use scenarios differed from that of other vertebrates, which suggests that reptiles may need to be given special consideration in land-use planning scenarios and that the use of faunal surrogates may not be appropriate for reptiles in all ecosystems.

The reptile assemblage in the northern extension of Suikerbosrand Nature Reserve appears to be sensitive to the changes that have resulted from previous agricultural land-use. The most palpable consequence of agricultural land-use is the homogenisation of the habitat, both in terms of vegetation monocultures and micro-habitat loss such as resulted from the removal of rocks prior to ploughing (D. Koen pers. comm.). The effect of rock removal appears to have led to a reduction in the number of captures of species that utilise rock outcrops for

basking, refuge and foraging e.g., *Cordylus vittifer* and *Aparallactus capensis* (Table 1). We found no difference in the structure of the vegetation between the traps placed in the three habitat types, which suggests that reptile diversity does not solely depend on physical characteristics of the vegetation, but may instead be linked to properties of the primary grassland communities that we did not assess e.g., percentage natural vegetation cover.

Measures of assemblage changes in response to habitat transformation are influenced by the strength and or proportion of positive, neutral and negative responses of the species within the assemblage. Certain species may benefit from the sharp edges created by disturbance e.g., lizards that use the edge to shuttle between sunlight and shade (Duelli 1997; Fabricius *et al.* 2003), while other species may suffer as a result of the reduced complexity of the habitat or vegetation (Maissoneuve & Rioux 2001; Jobin *et al.* 2004) or a reduction in natural vegetation (Lindenmayer *et al.* 2005; Hodgkison *et al.* 2007). The degree to which one is able to characterise the response of an assemblage is determined by the completeness of the sampling of that assemblage. Species richness estimates for the three habitat types in our surveys supported the observed differences in species richness between them. Estimates of species richness that utilise the ratio of singletons/unique to doubletons/duplicates are best considered as a lower bound of the total species richness (Mao & Colwell 2005). There have also been concerns raised regarding the truthfulness of the 95 % confidence intervals, as it can be shown that the number of undetected species may be very large without influencing the width of the confidence interval (Mao & Colwell 2005). For this reason we did not compare the estimated species richness for each of the three habitat types, we simply used the estimate to provide us with a measure of sample completeness. Mean estimates of sample completeness for the three habitats were

exceptionally high for the pristine and modified habitats, and more than satisfactory for the rocky habitat. The combination of high sample completeness and the observed differences in species richness of the three habitat types provide strong evidence of a significant decline in the species richness of the reptile assemblage following habitat transformation associated with cultivation.

Nucras lalandii (Lacertidae) appears to be highly sensitive to land-use change. All of the individuals of *N. lalandii* captured in our survey were captured at a single locality in a low, closed grassland (sensu Edwards 1983), with no captures recorded at the nearby modified site. Despite extensive surveys throughout Gauteng between 2000 and 2008, all five of the post-2000 localities for *N. lalandii* records are situated in primary grassland on the extension of Suikerbosrand Nature Reserve (Whittington-Jones *et al.* 2008). The population of *N. lalandii* in Suikerbosrand Nature Reserve is isolated from populations to the north and east by approximately 100 - 200 km (Jacobsen 1989; Jacobsen, 1995), and the species' absence in historically cultivated areas suggests that the species may be declining in Gauteng's highly-transformed landscape. Surprisingly, *N. lalandii* has not been recorded within the 1973 boundary of Suikerbosrand Nature Reserve despite surveys in 2004, 2005, 2006 and 2007 (Koen & du Toit 2007; Masterson 2007; Masterson *et al.* 2008) and the reasons for this absence are currently unknown. The persistence of *N. lalandii* in Gauteng may depend on the appropriate protection and management of primary grassland patches where the species occurs.

In contrast with the majority of reptile species observed during our study, *Trachylepis capensis* (Scincidae) appears to benefit from habitat transformation associated with cultivation. Even with the reduced species richness and reduced number of reptiles captured at the

modified sites, the majority of the *T. capensis* individuals captured during the survey were captured on the modified sites. For the majority of species, the number of captures recorded at the pristine or rocky sites was greater than or equal to the number captured on the modified sites. The number of captures of *T. capensis* at the modified sites may have been caused by an increase in the frequency or distance of movements by individuals and an associated increase in the probability of being captured. Alternately, *T. capensis* may actually be more abundant at modified sites than in the pristine or rocky habitats. In the pristine and rocky habitats, *T. capensis* may be affected by inter-specific competition with *Gerrhosaurus flavigularis* (Gerrhosauridae), which fills a similar ecological niche as *T. capensis*, and which occurs in greater numbers in these two habitat types than in the modified habitat. Whatever the reasons, the response of *T. capensis* to habitat transformation was exceptional among all the reptile species captured during our survey.

In systems where the natural vegetation plays an important role in faunal diversity, management actions that improve the condition of the vegetation can have positive spin-offs for the associated fauna (Castellano & Valone 2006), and vice versa (Santelmann *et al.* 2006). Currently the modified sites are dominated by weedy species, e.g. *Bidens pilosa* (blackjack), but a reseeding programme currently being implemented in the historically-cultivated areas of the extension to Suikerbosrand Nature Reserve is showing promising results in restoring the natural vegetation in these transformed areas (D. Koen, unpubl. data). Simultaneous monitoring of the vegetation and reptile assemblages on the extension of Suikerbosrand Nature Reserve would be useful in order to determine the effects of vegetation recovery on reptile species richness and composition.

In conclusion, we recommend that land-use planning in Gauteng emphasise the need for

areas of connected, untransformed habitat in order to mitigate the negative effects of habitat transformation on reptile assemblages. In the highly transformed landscape of Gauteng, the protection of untransformed habitat will play an important role in the persistence of species that are sensitive to disturbance e.g., *N. lalandii*. Where patches of primary grassland do not occur, disturbance management and habitat/vegetation restoration may be required to protect and/or restore key elements of the habitat. Currently it is not known whether the regeneration of natural vegetation will be sufficient to improve reptile diversity in the affected grasslands but regular monitoring of the reptiles at sites with regenerating vegetation is recommended.

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