

Effect of fire history and vegetation structure on herpetofauna in a South African grassland

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Abstract. Fire is a frequent feature of African grasslands and is commonly used in the management of conservation areas. We studied the herpetofaunal richness and composition of 10 sites to determine the effects of a 30-year fire management regime on the herpetofaunal assemblage in a reserve in South Africa. We trapped amphibians and reptiles during March and April 2004 at 10 sites with different fire histories. Sites of different post-fire ages were compared for differences in their species richness. We also measured the vegetation cover and vegetation height i.e. the vegetation structure at each of the sites surveyed. We found no significant effects of fire history on the species richness or composition of each site. Species composition at each site was better explained by post-fire age than by vegetation structure. There was a tight correlation between the vegetation cover of a site and its species richness, as well as a significant effect of vegetation structure on the similarity of the species found at each site. Vegetation structure appears to be the key factor affecting the structure of herpetofaunal assemblages in grasslands of South Africa, with fire and prescribed burning impacting on the assemblages via its effect on the vegetation.

Key words: Fire; herpetofauna; management practice; species composition; species richness; vegetation structure.

Introduction

Southern Africa is richly endowed with herpetofauna with many new, cryptic species discovered each year (Branch, 1998; 2001; Minter et al., 2004). Despite the region's herpetofaunal richness (>630 species) and high number of endemic species (>75%), ecological research on the herpetofauna lags far behind that of the more charismatic taxa such as birds and large mammals (Parr and Chown, 2003). Herpetofauna are known to be sensitive to habitat destruction and habitat modification (Jobin et al., 2004; Knapp, 2005), yet in a review of 66 fire ecology papers published in peer-reviewed journals on the southern African fauna, Parr and

Chown (2003) found that not a single study had tested the effect of fire or burning on amphibians and that only one of the papers focussed on a species of reptile (Testudinae: *Chersina angulata*; Wright, 1988). This is cause for concern because of the widespread use of fire as a conservation management tool, and its potential impact on the diversity of the herpetofauna.

Fire acts at many scales and modifies various aspects of the environment such as resource patchiness (Ross et al., 2002), microclimatic conditions (Cunningham et al., 2002) and habitat structure (Hailey, 2000). Use of fire as a management tool has created a fire-based paradigm for management of reserves and conservation areas in southern Africa (Parr and Brockett, 1999). Although there has been a recent shift towards patch-mosaic fire regimes, the prevailing fire management of conservation areas involves fixed mosaic (or rotational) fire management regimes (Parr and Brockett, 1999). Regulated fire regimes may bear little resemblance to the 'natural' fire regime of the area. The challenge for conservation managers is to identify the potential problems that the tools of management may create, especially in cases where such problems may go undetected for years or decades. This challenge is additionally complicated by the cryptic nature of herpetofauna (particularly reptiles) and the fact that we know little about their ecological optima and sensitivities.

In other parts of the world, research of the effects of fire on herpetofauna has progressed steadily, especially in the United States and Australia (e.g. Mushinsky, 1985; Lunney et al., 1991; Mushinsky, 1992; Greenberg et al., 1994; Ford et al., 1999; Cavitt, 2000; Hailey, 2000; Jones et al., 2000; Cunningham et al., 2002; Pilliod et al., 2003; Letnic et al., 2004; Woinarski et al., 2004; Kavanagh and Stanton, 2005). From the results of these studies, it is clear that the effects of fire on herpetofauna vary according to: fire size (Letnic et al., 2004); fire intensity (Hailey, 2000; Kavanagh and Stanton, 2005); season (Hailey, 2000); fire frequency (Cunningham et al., 2002; Mushinsky, 1992; Letnic et al., 2004; Woinarski et al., 2004); and the life history of the species concerned (Cunningham et al., 2002; Pilliod et al., 2003). What is not clear at this point is how extra-regional studies relate to the African arena, although they certainly provide a research template to evaluate the region-specific challenges of conservation and socio-economic development in Africa (e.g. Cowling et al., 2003).

Driver et al. (2005) have further highlighted the need for study by complete omission of data on reptiles from the National Spatial Biodiversity Assessment. In their analysis of the distribution of "species of special concern" in southern Africa, Driver et al. (2005) could only include information on birds, mammals, amphibians, butterflies, scorpions and dung beetles (Family: Scarabidae), as the data for reptiles are inadequate. In South Africa, there is also a disjunction between the distribution of bioregional programmes and the current and future threats to biodiversity. Anthropogenic threats to biodiversity are greatest in the northern and eastern parts of the country, while the majority of bioregional programmes are located in the southern parts, particularly the Cape Floristic Region (Driver et al., 2005). The necessity for ecologically-orientated studies on amphibians and

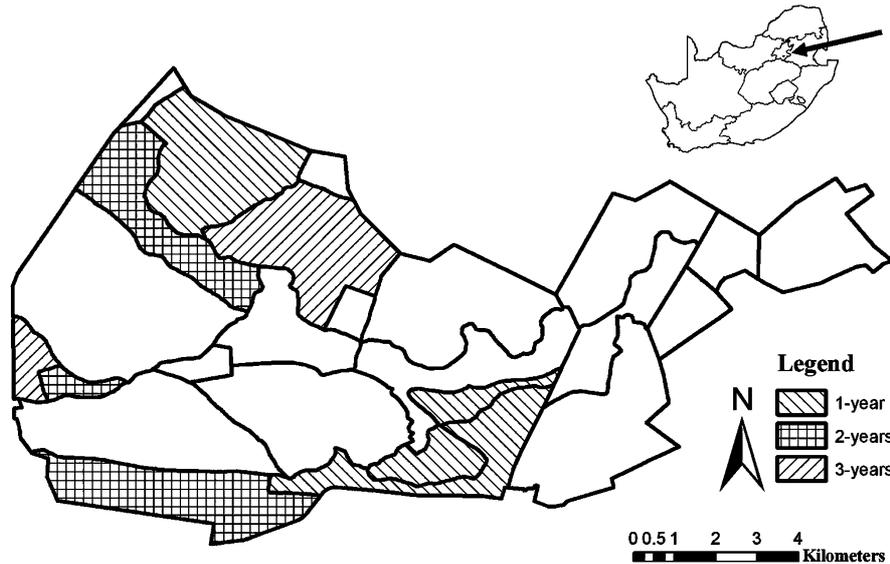


Figure 1. Map of the sampled burn-blocks of Suikerbosrand Nature Reserve, Gauteng, South Africa.

reptiles grows ever more urgent in the face of widespread habitat modification and increasing human pressure on natural resources in the country; particularly in the areas of highest human density such as in Gauteng Province.

During March-April 2004, we studied the effects of 30 years of management burns on the herpetofauna in Suikerbosrand Nature Reserve, Gauteng, South Africa; located in the fire-prone Highveld grasslands of South Africa (fig. 1). Grassland is the most threatened biome in southern Africa, with only 2% of the biome formally conserved and much of the area irreversibly transformed (Bredenkamp, 2002; Driver et al., 2005). Suikerbosrand Nature Reserve lies near the boundary of the Bushveld-Bankenveld and Moist Grassland priority areas, two of the highest priority areas for conservation in the region (Driver et al., 2005). The greatest threats to biodiversity of these areas is their crop potential and the likely spread of agricultural land use within them (Bredenkamp, 2002; Driver et al., 2005). We tested the hypothesis that patches with different fire histories have detectable differences in species richness and abundance of herpetofauna. We also investigated the effect of vegetation variables on similarity in species assemblages as an aid to understanding the basic ecological requirements of herpetofaunal communities in the grasslands.

Materials and Methods

Suikerbosrand Nature Reserve is located 50 km south of Johannesburg, Gauteng, South Africa. Established in 1974, the reserve encompasses the Suikerbosrand Mountain Range and is charged with conserving the mountain catchment and maintaining the biodiversity of the area. Rainfall is highly seasonal, with most of the

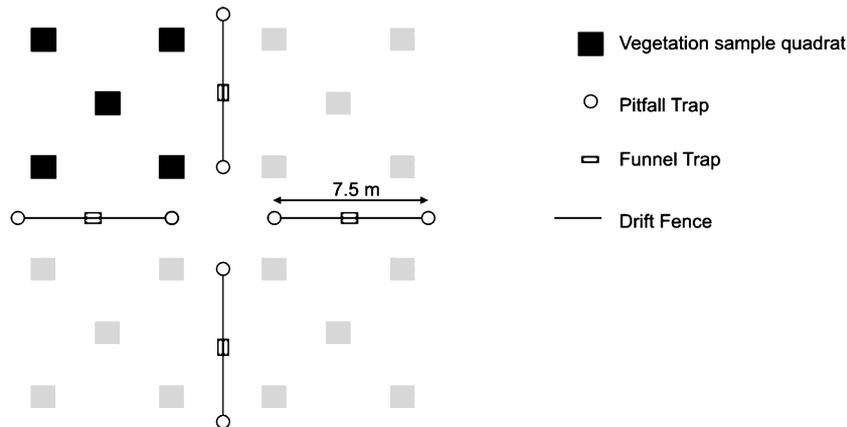


Figure 2. Plan diagram of the layout of each trap array showing also the positions of the vegetation quadrats used to sample the vegetation structure.

annual mean of 675 mm falling between October and March. The reserve consists of three vegetation types: Tsakane Clay Grassland, Andesite Mountain Bushveld and Gold Reef Mountain Bushveld (Mucina and Rutherford, 2004). Altitude ranges between 1545 and 1917 m.a.s.l. Fire management in the reserve involves the controlled burning of selected management blocks during August and September each year. Fire is used primarily to maintain the nutritional status of the vegetation for utilisation by the ungulate population of the reserve.

Terrestrial herpetofauna were sampled using an exploded cross design of four drift fences with eight funnel and eight pitfall traps (hereafter referred to as a trap array; fig. 2). Ten trap arrays were placed on nine management blocks (fig. 1). A single array was placed in each management block except for one of the three-year old sites, which had two trap arrays installed on it. This deviation in the sampling protocol was necessitated by a lack of three-year old management blocks due to numerous accidental and unplanned fires which prematurely burnt several management blocks in 2002.

Management blocks were selected to represent the widest possible fire return period (FRP) across each post-fire age class. Fire return period is defined as the average time interval between successive fires on a management block over the last 30 years. Due to a change in management practice during 2004, zero-year treatments were not available for us to sample. All trap arrays were set in the low-lying areas of Suikerbosrand Nature Reserve at elevations between 1554 and 1693 m.a.s.l. due to differences in the habitat characteristics of the plateau and the surrounding grasslands.

Each trap array consisted of four drift fences (7.5 m in length) separated by a 4 m space in the centre of the array (fig. 2). Drift fences consisted of semi-transparent plastic sheeting supported with 450 mm wooden stakes and were 250 mm tall. Pitfall traps (5-L and 10-L plastic buckets) were buried flush with the ground surface.

Funnel traps were constructed from wire gauze and were 450 mm × 150 mm (after Simmons, 2002). Funnel type and pitfall size were varied as part of another study (Maritz et al., 2007), but equal numbers of the four trap types were used at each array. Funnel traps were covered with grass for shading and wet sponges were placed into pitfall traps to prevent heat-related mortality of trapped animals.

All traps were checked twice daily (early morning and late afternoon) from 14 March 2004 to 14 April 2004, representing 4800 trap-days. All captured specimens were identified to species, measured (to nearest mm), weighed (to nearest 0.1 g), permanently marked and released within 30 m of point of capture. Specimens that could not be positively identified in the field were kept overnight for identification. Frogs and lizards were marked using toe-clipping while snakes were marked using ventral scale clipping as per Fitch (1987). A standard mark was used for all frogs and lizards. This allowed identification of recaptures but not individuals. Recaptured specimens were re-processed, but not re-marked.

At each trap array, we recorded the cover and height of vegetation in a stratified grid with the trap array at its centre (fig. 2). The characteristics of the vegetation at the trap array were representative of the vegetation of each management block. Vegetation height was measured at each of the four corners of the quadrat and 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. As vegetation cover was a proportional measure, we arcsine transformed these data prior to analysis.

Data analysis

Unless otherwise indicated, analyses were performed in Statistica version 6 (Stat-Soft, 2002). We tested for an effect of post-fire age on species richness using analysis of variance (ANOVA) for the three post-fire age classes (independent = post-fire age; dependent = species richness). Using linear regression analysis, we compared the univariate impacts of FRP, vegetation cover (arcsine transformed) and vegetation height on species richness. There was a significant correlation (Pearson's correlation: $r > 0.79$) between post-fire age and vegetation cover and post-fire age and vegetation height thus a model including these factors would have been strongly autocorrelated. Accordingly, we built and compared two models for predicting herpetofaunal species richness. Model 1 included vegetation type, post-fire age and FRP, while model 2 included vegetation type, vegetation cover, vegetation height and FRP.

We analysed the species similarity of our 10 survey sites using the Analysis of Similarity (ANOSIM) subroutine in PRIMER 5 (Clarke and Gorley, 2001). ANOSIM is a non-parametric procedure that compares within-factor species similarity with the between-factor species similarity. Due to sample size restrictions, we compared the similarity of the entire herpetofaunal assemblage at each site. We used ANOSIM to analyse the effects of three factors: (1) post-fire age, (2) vegetation structure and (3) vegetation type (table 1). In the ANOSIM by vegetation

Table 1. Details of the 10 sites selected for the placement of trap arrays during March/April 2004.

Site	Years since previous burn (year burnt)	Average fire-return period between 1973 and 2003 (years)	Vegetation type ^b	Vegetation group ^c
1	1 (2003)	2.5	Tsakane Clay Grassland	1
2	1 (2003)	3.4	Andesite Mountain Bushveld	1
3	1 (2003)	5	Tsakane Clay Grassland	1
4	1 (2003)	5.4	Tsakane Clay Grassland	2
5	2 (2002)	1	Tsakane Clay Grassland	2
6	2 (2002)	3.5	Andesite Mountain Bushveld	2
7	2 (2002)	3.7	Andesite Mountain Bushveld	3
8	3 (2001)	2.8	Andesite Mountain Bushveld	3
9 ^a	3 (2001)	3.6	Tsakane Clay Grassland	3
10 ^a	3 (2001)	3.6	Tsakane Clay Grassland	3

^a In same management block.

^b According to Mucina and Rutherford (2004).

^c According to fig. 3.

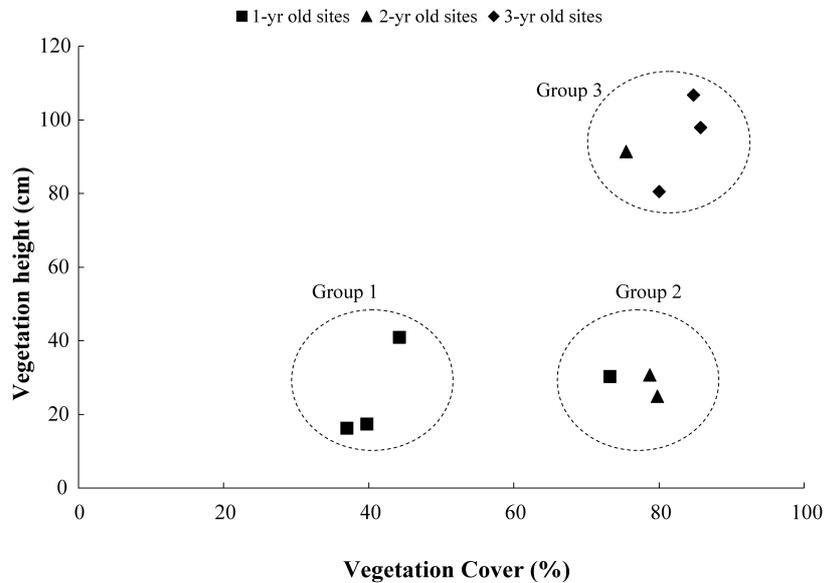


Figure 3. The average vegetation cover and vegetation height of each site. The graph shows the grouping of the sites used in the analyses of species similarity.

structure, the 10 sites were assigned to three groups based on average vegetation height relative to average vegetation cover (fig. 3).

For our similarity index, we used the Chao-Sørensen Abundance-based Estimator of Similarity (Chao et al., 2005). This estimator of similarity is better able to predict shared *unseen* species than the classic Sørensen index and can thus provide a more realistic measure of species similarity (Chao et al., 2005). It is this ability

to predict shared unseen species that makes it particularly useful as a species similarity measure for reptile surveys because numerous species may be represented by only one or two individuals due to their cryptic nature or low densities. We used EstimateS version 7.5.0 (Colwell, 2005) to calculate the Chao-Sørensen Abundance-based Estimator of Similarity for our sites' abundance data. For this survey, we classified rare species as those with less than three captures in the entire survey period (although the EstimateS default is 10 captures). We then imported this similarity matrix into PRIMER 5 (Clarke and Gorley, 2001) and ran the ANOSIM procedures.

In addition to the ANOSIM, we used Nonmetric Multidimensional Scaling (NMS), with the Chao-Sørensen Abundance-based Estimator of Similarity distance measure, to explore the effects of post-fire age and vegetation structure on the similarity of the herpetofaunal assemblages at each site.

Results

A total of 82 frogs from six species, 47 lizards from five species and 19 snakes from eight species, were captured during the survey. The most abundant species recorded during the survey were *Gerrhosaurus flavigularis* (yellow-throated plated lizard), *Schismaderma carens* (red toad), *Tomopterna cryptotus* (tremolo sand frog) and *Amietophrynus gutturalis* (guttural toad; table 2). The combined species richness for all sites in each post-fire age class ranged from 12-13 species, although the average species richness per trap array in each post-fire age class ranged from 5-6.7 species.

Site species richness was not well explained by post-fire age (ANOVA, $F_{2,7} = 1.72$, $P = 0.25$), FRP (regression, $F_{1,8} = -0.91$, $P = 0.39$, $R^2 = 0.094$), vegetation type (ANOVA, $F_{1,8} = 1.32$, $P = 0.28$) or average vegetation height (regression, $F_{1,8} = 1.10$, $P = 0.302$, $R^2 = 0.132$). Frog species richness was significantly higher on the two-year old sites (ANOVA, $F_{2,7} = 7.15$, $P = 0.02$). The number of frog captures at the two-year old sites was also greater than that of the other age classes (table 2), but not significantly so (ANOVA, $F_{2,7} = 1.89$, $P = 0.22$).

There was, however, a strong correlation between a site's vegetation cover and its species richness (regression, $F_{1,8} = 3.75$, $P = 0.0063$, $R^2 = 0.627$; fig. 4). The only species for which more than five captures were recorded in each age class was *G. flavigularis*. An analysis of the mean number of captures at each site in each age class found no significant difference between the number of captures of each age-class (ANOVA, $F_{2,7} = 0.57$, $P = 0.59$).

A comparison of the two predictive models revealed that model 1 (vegetation type, post-fire age and FRP) was not as useful as model 2 (vegetation type, vegetation cover, vegetation height and FRP) in predicting species richness. Vegetation type, post-fire age and FRP were all non-significant and it was only the interaction of vegetation type and post-fire age that approached statistical significance. Of all the

Table 2. A summary of the total number of captures and recaptures for each species recorded and the breakdown of captures for each species by post-fire age class during March/April 2004.

Species	Number captured	Number recaptured	Post-fire age			
			One year	Two years	Three years	
Frogs						
Bufonidae						
<i>Amietophrynus gutturalis</i>	17	2	14	1	2	
<i>Schismaderma carens</i>	21	–	1	20	–	
Hyperoliidae						
<i>Kassina senegalensis</i>	6	1	–	6	–	
Pyxicephalidae						
<i>Cacosternum boettgeri</i>	15	–	–	5	10	
<i>Tomopterna cryptotus</i>	19	–	–	17	2	
<i>Tomopterna natalensis</i>	4	–	2	2	–	
Sub-total	82	3	17	51	14	
Lizards						
Agamidae						
<i>Agama aculeata distanti</i>	1	–	1	–	–	
Lacertidae						
<i>Gerrhosaurus flavigularis</i>	27	–	7	12	8	
Scincidae						
<i>Panaspis wahlbergii</i>	3	–	1	–	2	
<i>Trachylepis capensis</i>	10	–	4	4	2	
<i>Trachylepis varia</i>	6	–	1	–	5	
Sub-total	47	0	14	16	17	
Snakes						
Colubridae						
<i>Aparallactus capensis</i>	3	–	2	–	1	
<i>Crotaphopeltis hotamboeia</i>	4	–	–	2	2	
<i>Dasypeltis scabra</i>	2	–	1	–	1	
<i>Lamprophis aurora</i>	3	–	–	1	2	
<i>Psammophis crucifer</i>	2	–	1	1	–	
<i>Pseudaspis cana</i>	1	–	1	–	–	
Elapidae						
<i>Hemachatus haemachatus</i>	1	–	–	–	1	
Viperidae						
<i>Causus rhombeatus</i>	3	–	1	2	–	
Sub-total	19	0	6	6	7	
Total	148	3	37	73	38	

factors in model 2, only vegetation cover was significant in all model combinations and was thus the only factor selected for use in the final model (GLM, $F_{1,8} = 13.5$, $P = 0.0063$, $R^2 = 0.628$).

The results of our ANOSIM indicated a near-significant effect of post-fire age on species similarity (ANOSIM, $Global R = 0.313$, $P = 0.051$). The greatest dissimilarity in species composition and abundance was between the two-year

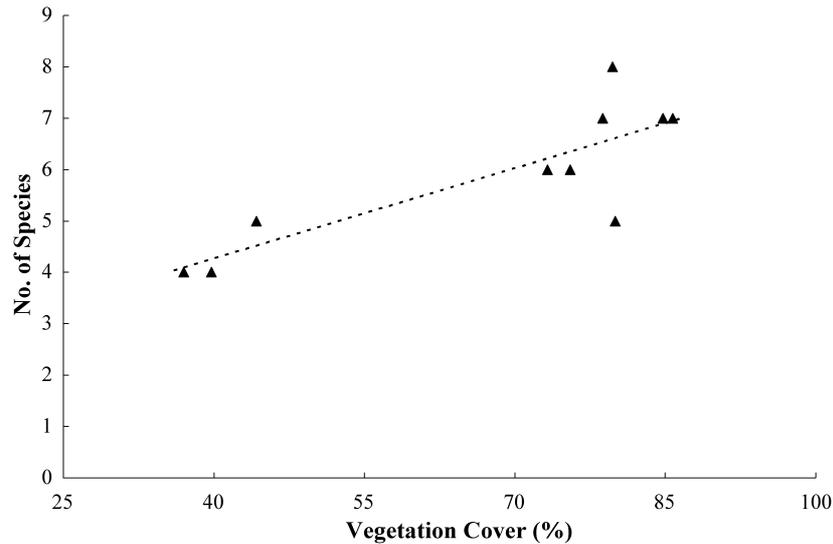


Figure 4. The relationship between species richness and vegetation cover for the sites surveyed during March/April 2004.

and three-year old sites. When we analysed the species similarity between the three groups of vegetation structure (fig. 3), the ANOSIM indicated a significant difference in the similarity of the vegetation groups (ANOSIM, *Global R* = 0.361, *P* = 0.049). Sites in group 3 (high vegetation cover and tall grass) were highly dissimilar to the sites in the other two groups. By contrast, sites in group 1 and group 2 were very similar to each other.

The NMS ordination of the sites in two dimensions is shown in fig. 5. From the 31 iterations needed for the ordination to converge, the final stress of the solution was 0.106. The three-year old sites clustered as a distinct group while there was only minimal overlap between the one-year and two-year old sites (fig. 5). The clustering of the sites according to vegetation groups (the number in parentheses), was less distinct and indicates that the post-fire age was an important factor in the similarity of the herpetofaunal assemblages between sites.

Discussion

Our data indicate that herpetofaunal species richness and assemblage composition are linked to vegetation structure in the grasslands of Suikerbosrand Nature Reserve. Of the factors considered in our study, the best predictor of species richness at each site was the vegetation cover. Vegetation structure was also an important factor affecting species similarity between the sites surveyed. Post-fire age was not a good predictor of species richness, despite the well-established link between fire and vegetation structure (Cunningham et al., 2002; Hudak et al., 2004; Sawadogo et

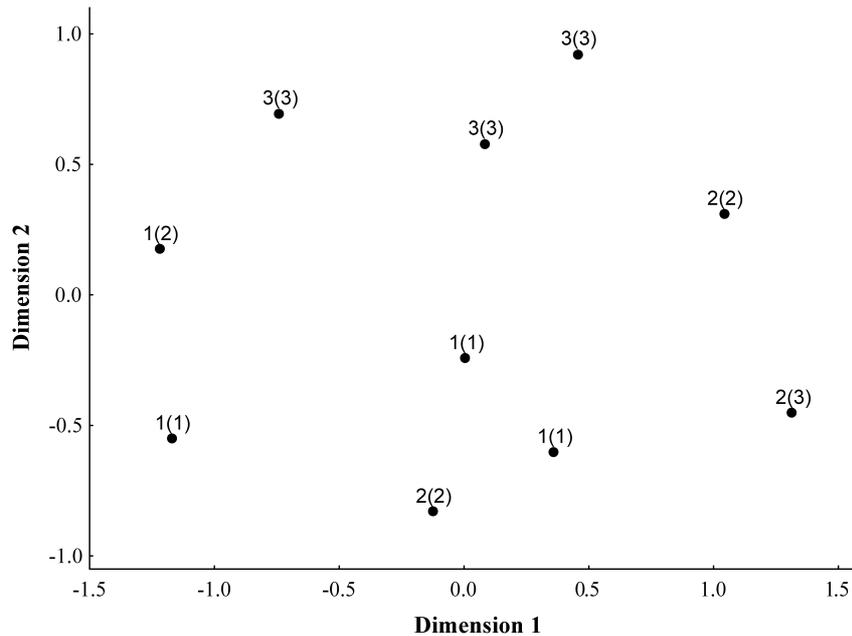


Figure 5. Nonmetric Multidimensional Scaling ordination of the herpetofaunal assemblages at the 10 sites. In the labels, the first number is the site's post-fire age, while the number in parentheses is the site's vegetation group from fig. 3.

al., 2005; Masterson, unpublished data), yet was a factor affecting species similarity between sites according to our NMS ordination.

We studied the response of the herpetofaunal assemblage to the current fire regime employed in and detected no differences in species richness. This does not preclude the possibility of species-specific negative responses to the current management practices and it should be noted that the lack of adequate baseline information limits the scope of our study. Without information about the species richness for our sites prior to management actions, we can only conclude that the within-management fire regime is not the primary driver of herpetofaunal species richness. According to our results, the *de facto* driver of species richness is the vegetation cover at each site.

The link between a site's fire history and its vegetation cover is not consistent between sites. The rate of regrowth following a disturbance is related to the timing of disturbance (Culvenor, 1993), the amount of rainfall (Peake et al., 1979; Keya, 1997) and the soil conditions (de Rouw, 1994). Thus, if the variables of cover and height are treated as ecological "distance" measures (i.e. vegetation cover and height indicate the progression of the site's recovery since the fire), it is evident that it is not the chronology (post-fire age) that is important in predicting species richness, but rather the degree of regeneration of the vegetation.

From a species similarity perspective the results are similar, yet subtly different. Species similarity between the sites in vegetation group 3 was significantly greater than the between-group comparisons with vegetation group 1 and vegetation

group 2, which suggested that vegetation structure was the main factor affecting species similarity. However, the results of the NMS ordination suggested that post-fire age cannot simply be discarded as a factor. The NMS plot revealed that the best explanation for the clustering of sites was their post-fire age, which lends extra support to the near significant result of the ANOSIM for post-fire age. Thus it is necessary to review the processes affecting species richness measures and species similarity between sites.

A species richness measure is determined by the detection of species at each site. For passive trap arrays, detection probability increases with increased activity of individuals of each species (Cavitt, 2000). It is therefore reasonable that vegetation structure would affect species activity, due to its effects on the risk of predation and the thermal microclimate, as has been suggested by Wilgers and Horne (2006). In their study of recently burnt areas, Wilgers and Horne (2006) found that coverboards detected more herpetofaunal species than trap arrays, and hypothesised that the cover provided by the coverboards compensated for the absence of covering vegetation and resulted in the increased use of the coverboards as a retreat. The non-use of coverboards in our survey may have resulted in an underestimate of species richness in areas of low vegetation cover (Wilgers and Horne, 2006). Alternately, records from trap arrays may more accurately reflect the species present due to the reduced detection of vagrant species that only cease moving across a burnt or open area due to the cover afforded by the coverboards.

By contrast, an abundance-based measure of species similarity is dependent on the number of records for each species. When using trap arrays, the effect of activity patterns on the recorded numbers of individuals per species is either exacerbated or mitigated by the density of the individuals per site (Brose et al., 2003). If activity patterns remain relatively constant between sites, then we expect similar assemblages to result in a similar number of records per species (Brose et al., 2003; Brose and Martinez, 2003). Thus the observation that post-fire age classes clustered together more closely than sites in the same vegetation groups suggests that post-fire succession is a factor in the herpetofaunal communities sampled.

Letnic et al. (2004) found that post-fire succession in lizard habitats depended on the regeneration of the vegetation. Additionally, early-succession lizard species were those that could tolerate high temperatures, construct burrows and use bare ground for territorial displays (Letnic et al., 2004). Late-succession lizard species were less tolerant of high temperatures, poor burrowers and use the shade of the vegetation for thermoregulation (Letnic et al., 2004). The lower species richness of the herpetofaunal assemblages in areas with poorly-developed vegetation structure has two possible explanations. Firstly, the species are not present in these recently-disturbed areas, due to either fire-induced mortality (Wright, 1988) or site avoidance behaviour (Twigg and Fox, 1991). Alternatively, the species are present at the sites but are not recorded due to reduced levels of activity that result from low thermoregulatory flexibility (e.g. Letnic et al., 2004) or increased exposure to predators (e.g. Towns and Elliott, 1996).

The strong relationship between a site's vegetation cover and species richness in our study suggests that vegetation cover relieves some of the stressors of species in the herpetofaunal assemblage. The consequent higher levels of activity improve the detection probability of the species present at each site and may be the sole cause of the higher species richness observed. Alternatively, the colonisation of disturbed sites may occur at a rate similar to the re-establishment of the vegetation after fires. Following a period of reproduction and population growth at each site, the detection probability of each species will be greater than that of species with small population sizes. If this alternate hypothesis is true, it would be expected that initial colonisation of the site should be followed by a stabilisation in its species composition. The relationship between post-fire age and similarities in species composition supports this hypothesis.

The strong correlation between vegetation cover and species richness raises some interesting questions. If we assume that the relationship between vegetation structure and herpetofaunal richness and composition is causal, then we would expect fire to have an initial proximal impact that is only detectable within a certain period of time immediately following the disturbance. In addition to this, we would expect that other factors such as grazing, which may modify the structure of the vegetation (e.g. Keya, 1997), would also affect herpetofaunal richness and composition. The impacts of grazing intensity on herpetofauna are complex and variable. Some studies report a decrease in reptile richness and abundance with no apparent effect on amphibians (e.g. Woinarski and Ash, 2002) and some report different responses for subsets of the herpetofaunal assemblage (e.g. James, 2003). Heavily grazed sites should deviate from the expected pattern of post-fire vegetation regeneration and provide opportunities for further investigation of the relationship between the herpetofauna and vegetation structure. A carefully designed experiment, for which good baseline data on herpetofaunal richness and abundance are available, could be used to separate the effects of fire and vegetation cover.

Our study highlights the need for further research on the effects of management practices on the herpetofauna in southern Africa — here we have only begun to tackle the complexity of these relationships. We also emphasise the need for studies in other fire-prone systems such as Fynbos and Savanna biomes, with a view of establishing monitoring programs in each. The development of long-term monitoring programs are essential for improving our understanding of natural variation in herpetofaunal communities, classifying the potential responses of herpetofauna to disturbance, and identifying species that are under greater threat than is currently understood. Long-term monitoring programs are also vital in the formulation of “herpetofauna-friendly” conservation management plans, particularly in instances where the herpetofauna is under obvious threat from habitat transformation.

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