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# Effects of bush encroachment on an assemblage of diurnal lizard species in central Namibia

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**Abstract**

Bush encroachment is a serious environmental and economic problem in Namibia, but little is known about impacts on native reptile diversity. Area-confined visual surveys were used to examine a diurnal lizard assemblage in central Namibian commercial ranchlands. Surveys were conducted in plots of open savanna habitat and proximal bush-encroached habitat. The following four species comprised 97.5% of all lizard observations: *Pedioplanis undata*, *Mabuya varia*, *M. striata*, and *Lygodactylus bradfieldi*. *Pedioplanis undata* was terrestrial, and the remaining three species were largely arboreal in our study plots. *Mabuya varia* was found in all savanna plots but was absent from all bush-encroached plots. Two species (*P. undata* and *L. bradfieldi*) were less abundant in bush-encroached plots. One species (*M. striata*) was more abundant in bush-encroached plots than in open savanna plots. Arboreal lizards demonstrated an avoidance to invasive woody plant species. Decreased diversity of habitat structure in bush-encroached habitats appears to influence native savanna lizard assemblages. Our results are consistent with accumulating evidence suggesting that bush encroachment and its associated ecological impacts are reorganizing savanna ecosystems throughout southern Africa.
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*Keywords:* Lizards; *Mabuya*; *Pedioplanis*; *Lygodactylus*; Bush encroachment; Savanna; Habitat change; Namibia; Africa

## 1. Introduction

Although humans have influenced the natural environment in Namibia for thousands of years, changes in land use practices over the last century have severely altered natural ecological processes (Louw and Seely, 1982; Prins and van der Jaeugd, 1993; Hoffman, 1997; Pallett, 1997). Recent human-mediated impacts include overgrazing, fire suppression, fragmentation of historical migration routes, establishment of permanent water sources and extirpation of the largest herbivores and top carnivores (for a review, see Barnard, 1998). A consequence of these ecological changes is the conversion of savannas to dense, acacia-dominated thickets with little grass cover, a process known as "bush encroachment." This problem is especially prevalent on commercial ranchlands in central Namibia, to the extent that bush encroachment has measurably reduced the economic productivity of the Namibian livestock industry (Quan et al., 1994).

Livestock grazing has been the predominant land use practice in Namibia for several centuries; consequently, much of the native wildlife in Namibia (and throughout much of sub-Saharan Africa) must coexist with livestock production (Kinahan, 1991; Mabutt, 1994; Archer, 1995). Nevertheless, commercial ranchlands in Namibia still harbor a diverse assemblage of native species and have substantial potential as refuges for Namibia's biota. For example, the majority of Namibia's populations of native large ungulates (over 70%) and the largest remaining population of cheetahs in the world are found on commercial ranchland, outside of the formal protected area network (Joubert and Morsbach, 1982; Marker-Kraus et al., 1996). Considerable conservation efforts and government wildlife policies are focused on these large mammalian species (reviewed by Griffin, 1998, and Richardson, 1998). While these

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efforts complement biodiversity conservation objectives in most cases (e.g. the cheetah, see Marker-Kraus et al., 1996), some less economically measurable and/or popular components of biodiversity may not be compatible with a system designed to promote livestock production and large, huntable game (Richardson, 1998). Most of the native species that do not have direct economic value in Namibia are found outside of the formal protected area network (Barnard et al., 1998). A better understanding of interactions between native species and human impacts is an important step towards native species conservation on commercial ranchland.

Here we present results of systematic surveys of an assemblage of lizard species in open savanna and bush-encroached habitats in central Namibia. Our purpose was to examine lizard species composition, relative abundance, and microhabitat use in open savanna and bush-encroached habitats. In a review of resource partitioning among species of amphibians and reptiles, Toft (1985) found habitat to be more important than temporal or dietary dimensions in interspecific separation. Patterns in the spatial use across habitat gradients by lizard assemblages have been well documented, yet few studies have examined the impacts of ecological processes on lizard assemblage stability at the landscape scale (Case, 1994; Vitt, 1994; but see Pianka, 1996). Although lizards have little direct economic value, they are important components of Namibian savannas and may be impacted by bush encroachment. We compared lizard assemblages associated with open savanna and bush-encroached habitat and interpreted our results with respect to accumulating evidence that bush encroachment and its associated ecological impacts are reorganizing savanna ecosystems throughout southern Africa.

## 2. Methods

### 2.1. Study area

The study area is located on ranchland owned by Cheetah Conservation Fund (CCF) in central Namibia, approximately 30 km east of Otjiwarongo (16° 39′ 0″ E, 20° 28′ 12″ S). Dominant topographic relief within the study area is in the form of small (~1–8 ha), isolated granitic outcrops (kopjes). These outcrops rise above a surrounding matrix of flatland, which has virtually no exposed rock. The Waterberg Plateau, a 4100-km$^2$ sandstone uplift, lies on the southern periphery of the study area and is the dominant geological feature of the region. The study area is semi-arid and lies between the 400 and 450 mm annual rainfall isopleths. There is marked seasonality with most rainfall occurring between November and April. The wet season is pronounced and characterized by extensive thundershowers and flooding, with considerable variation in the amount of precipitation between years (Barnard, 1998).

The region is situated in the Thornbush Savanna vegetation zone defined by Geiss (1971). Vegetation is typical of xeromorphic thornbush savanna with dominant woody plant genera consisting of *Acacia*, *Dichrostachys*, *Grewia*, *Terminallia*, and *Boscia*. Understory vegetation is relatively sparse, although ephemeral forbs are present following rain. This region has been extensively modified over the last century through human-mediated causes compounded by natural climatic fluctuations (Louw, 1982; Prins and van der Jaeugd, 1993; Hoffman, 1997; Pallett, 1997). Some native woody species such as *A. mellifera*, *A. tortillis*, and *D. cinerea* have proliferated, and perennial grasses have been reduced throughout this area (Bester, 1996; Rhode, 1997) to the extent that remnant patches of historic open savanna habitat exist only where livestock grazing has been limited.

### 2.2. Field methods

Six 1-ha plots were established in open savanna ($n=3$) and proximal bush-encroached habitat ($n=3$). Savanna and bush-encroached plots were established in areas of similar soil types, but differing management and land-use histories. Interviews with local farmworkers and former landowners (R. Jeo, unpublished data) indicate that bush-encroached plots had been comprised of savanna-like vegetation within the previous 20 years, but have since been subjected to continual heavy livestock grazing pressure and were subsequently invaded by woody *Acacia* and *Dichrostachys* species. Invasion of these woody species was concomitant with reduction of perennial grass cover. Savanna plots were located in an area that had not been grazed by livestock for the past 10–15 years and had experienced a natural fire within the last 20 years (L. Marker, personal communication).

Eight visual surveys for diurnal lizards were conducted in each plot between late October and December, 1999. We used time-constrained, area-constrained survey techniques (Heyer et al., 1994). A survey lasted 1 h and consisted of two observers walking along parallel transects, each ten meters in width. This method allowed us to consistently observe and accurately identify lizard species in both habitats. The same observers were present during each survey to maintain consistent observer bias between plots. One species (the gecko *Lygodactylus bradfieldi*) is smaller and less conspicuous than the other species. Although we suspect that we underestimated the abundance of this species in relation to the other species surveyed, we are confident that our observations of *L. bradfieldi* between habitats were consistent. Plots were surveyed between 0900 and 1800 hours and between temperatures of 28 and 37° C. Plots were not surveyed during inclement weather (i.e. rain or excessive wind) and no plot was sampled more than once on a given day. Because plots were surveyed repeatedly, we elected to minimize habitat disturbance and included only lizards readily visible; we did not disturb cover objects in our study plots. For plots in which they occurred, each of the four most common species encountered (see later) was initially observed during the first or second of the eight surveys.

For each lizard observed, we recorded the microhabitat with which it was associated. Because of the limited structural diversity in both open savanna and bush-encroached savanna, we classified microhabitat into only four categories: downed wood/snags; standing wood (living or partially dead); termitaria; and open ground. With the exception of *Agama aculeata*, which was observed in small numbers, lizards were not found to use termitaria and we thus excluded this variable from microhabitat analysis. Trees constituting standing wood were identified to species and assigned to a size-class with respect to height (0–1 m, 1–3 m, and >3 m).

We characterized the macrohabitat of each plot by quantifying the following habitat variables: percent perennial grass, percent downed wood, percent termitaria, percent canopy cover, and woody species composition and size-class. Percent downed wood and termitaria were estimated to $m^2$ using the entire 1-ha plot as a sampling unit. All other variables were quantified within eight circular subplots ($r = 5.7$ m) laid out along four transects in each plot for ordered sampling.

### 2.3. Data analysis

We pooled species observations in replicate plots of each habitat to compare species assemblages between open savanna and bush-encroached habitat types. In combining samples, we assumed that each plot was representative of its respective habitat type. A chi-square test of independence was then used to test homogeneity of species assemblages between the two habitat types. We estimated relative abundances of lizard species by calculating observations per survey hour (OSH) for each species in each plot. Means of species abundances were thus obtained for each habitat type. We compared proportions of each lizard species in both habitats by constructing 95% confidence intervals for the differences between the two proportions. Stepwise regression analyses were used to quantify macrohabitat associations of each species using habitat data collected for each plot ($P < 0.05$ for entry into the model). Preferences of arboreal lizards for tree species and tree size classes were calculated using the selection index of Manly et al. (1993). The selection index equals the proportion of arboreal lizard observations assigned to the resource (tree species or size class), divided by the proportional availability of the resource. The standardized selection index presents these ratios in a standardized form such that the ratios sum to 1.0 over all resource types. A preference value is obtained based on the number of available resource categories.

## 3. Results

### 3.1. Habitat comparison of savanna and bush-encroached plots

Compared to open savanna plots, bush-encroached plots were visually different (Fig. 1; Table 1). Bush-encroached plots were characterized by having a different assemblage of woody plant species (Table 2), greater density of woody plants ($x = 309$/ha vs. 217/ha), greater degree of canopy cover, greater amount of downed wood, and lesser amount of perennial grass cover. Bush-encroached plots also differed strikingly from open savanna plots in that there was increased homogeneity in the spatial extent of woody plant cover.

Fig. 1. Representative photographs of savanna (Plot 2; left) and bush-encroached (Plot 5; right) habitats demonstrating differences in vegetation in our study. In the savanna photograph, the largest tree in the foreground is *Acacia erioloba*, the two smaller trees behind, and to either side of it, are *A. mellifera*. The trees in the bush-encroached plot are predominantly *Dichrostachys cinerea*.

Table 1
Summary data on lizard abundances and habitat variables for the six plots surveyed[a]

| Plot | *Pedioplanis undata* | *Lygodactylus bradfieldi* | *Mabuya striata* | *Mabuya varia* | Perennial grass cover | Canopy cover | Termitaria cover | Downed wood |
|---|---|---|---|---|---|---|---|---|
| 1 | 4.13 | 0.50 | 0.88 | 0.75 | 37.5% | 22.5% | 0.14% | 0.23% |
| 2 | 2.88 | 4.36 | 0.00 | 0.75 | 45.0% | 18.0% | 0.04% | 0.43% |
| 3 | 3.75 | 3.75 | 0.38 | 1.38 | 32.5% | 26.5% | 0.25% | 0.45% |
| 4 | 0.00 | 1.38 | 4.25 | 0.00 | 12.5% | 37.5% | 0.27% | 3.11% |
| 5 | 0.75 | 1.75 | 1.38 | 0.00 | 8.0% | 54.0% | 0.20% | 2.82% |
| 6 | 2.00 | 0.13 | 3.88 | 0.00 | 12.5% | 52.5% | 0.26% | 2.96% |

[a] Lizard abundances are in observations/survey hour. Plots 1–3 were savanna habitat and Plots 4–6 were bush-encroached habitat.

Table 2
Woody plant species composition in savanna and bush-encroached plots

| Taxa | Savanna (Plots 1–3) | | Bush-encroached (Plots 4–6) | |
|---|---|---|---|---|
| | Mean density/ha | Proportion of woody plant composition | Mean density/ha | Proportion of woody plant composition |
| *Acacia erioloba* | 31 | 0.14 | 0 | 0 |
| *A. fleckii* | 39 | 0.18 | 0 | 0 |
| *A. hebeclada* | 4 | 0.02 | 35 | 0.11 |
| *A. mellifera* | 40 | 0.19 | 28 | 0.09 |
| *A. refisciens* | 23 | 0.11 | 12 | 0.04 |
| *A. tortillis/karoo* | 0 | 0 | 97 | 0.31 |
| *Dichro. Cinerea* | 53 | 0.25 | 74 | 0.24 |
| *Grewia* spp | 19 | 0.09 | 17 | 0.05 |
| *Ziziphus* spp | 3 | 0.01 | 24 | 0.08 |
| *Combretum* spp. | 3 | 0.01 | 21 | 0.07 |
| *Rhigozum* spp. | 1 | <0.01 | 1 | <0.01 |
| *Boscia* spp. | <1 | <0.01 | <1 | <0.01 |
| *Commiphora* spp. | 0 | 0 | <1 | <0.01 |

### *3.2. Comparison of lizard assemblages between savanna and bush-encroached plots*

A total of 320 lizard observations were made during 48 survey-hours, representing four families and seven species. Two additional species, *Varanus albigularis* (Varanidae) and *Mabuya capensis* (Scincidae) were observed in similar habitat near our plots. Rocky habitats in the study area supported different lizard assemblages that included some species observed in open savanna and bush-encroached habitats. The species *Lygodactylus bradfieldi* (Gekkonidae), *Mabuya striata*, *M. varia* (Scincidae), and *Pedioplanis undata* (Lacertidae) accounted for 97.5% of our observations. The nocturnal *Pachydactylus turneri* (Gekkonidae), and the diurnal species *Agama aculeata* (Agamidae) and *Nucrus intertexta* (Lacertidae), accounted for the remainder of observations. These latter three species were not included in our analyses.

Diurnal lizard species in bush-encroached habitat represent a subset of lizard species occurring in open savanna. Although plots may not be true replicates (sensu Hurlbert, 1984), similar species composition between bush-encroached and savanna habitats indicates that examining differences in the assemblages is valid. Species assemblages, based on relative abundances of each species, differed between the bush-encroached and savanna habitats ($X^2 = 123.0914$, d.f. = 3, $P < 0.001$; Fig. 2). Both *Pedioplanis undata* and *Lygodactylus bradfieldi* were more abundant in savanna. For *P. undata* this difference was by a factor of 3.9 (3.58 OSH in savanna versus 0.92 OSH in bush-encroached, 95% confidence interval; $0.18 \leqslant \theta \leqslant 0.38$), whereas for *L. bradfieldi* this difference was by a factor of 2.7 (2.88 OSH in savanna versus 1.08 OSH in bush-encroached, $0.06 \leqslant \theta \leqslant 0.26$). *Mabuya varia* was observed in all savanna plots (0.96 OSH), but was absent from all bush-encroached plots. *Mabuya striata* was the only species surveyed that was more abundant in bush-encroached plots than savanna plots. This difference was by a factor of 7.5 (3.17 OSH in bush-encroached versus 0.42 OSH in savanna plots, $0.47 \leqslant \theta \leqslant 0.65$).

We found some associations between macrohabitat variables and lizard abundances (Table 3). *Pedioplanis undata* and *Mabuya varia* were negatively associated with downed wood, while *M. striata* was positively associated with downed wood. Additionally, *M. varia* was positively associated with termitaria. No habitat

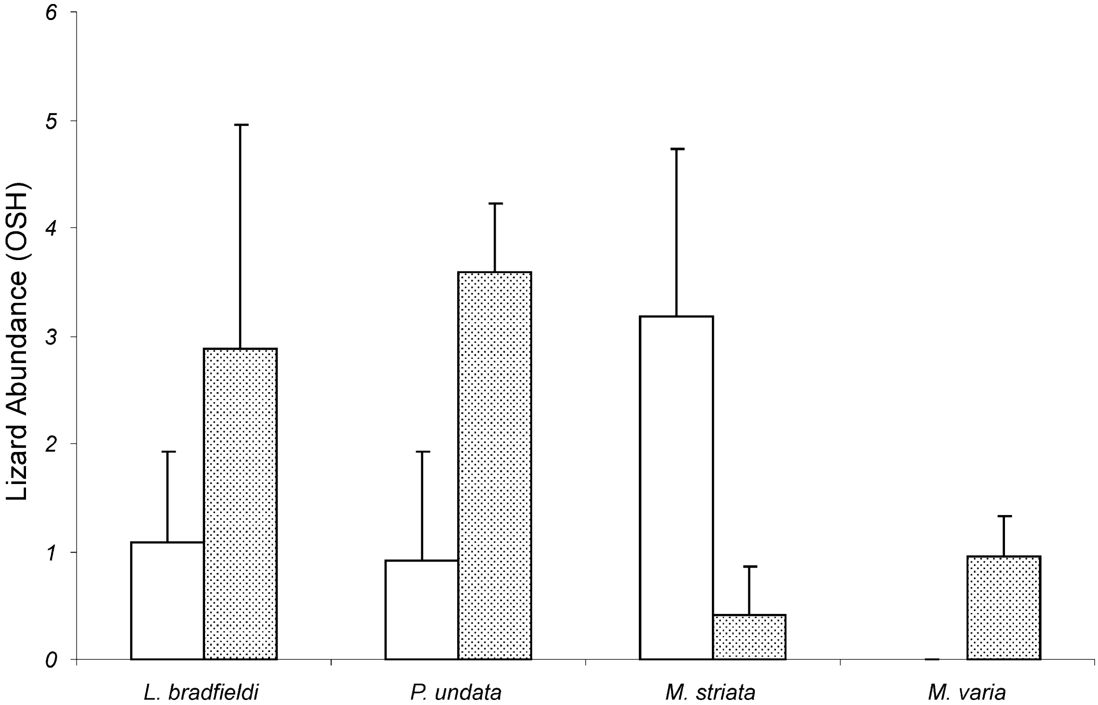

Fig. 2. Mean abundance of each lizard species in savanna (stippled bars; $n=3$ plots) and bush-encroached (open bars; $n=3$ plots) habitats. Error bars indicate standard deviation. OSH = observations per survey hour.

Table 3
Results of stepwise linear regression analysis; no habitat variable met the significance level for entry into the model for *Lygodactylus bradfieldi*

| | $R^2$ | d.f. | *F*-value | *P*-value | Parameter estimate |
|---|---|---|---|---|---|
| *Pedioplanis undata* | 0.82 | 4 | 17.76 | 0.0135 | |
| Intercept | | | | | 32.00128 |
| Downed wood | | | | | −8.34077 |
| *Mabuya striata* | 0.72 | 4 | 10.25 | 0.0329 | −0.02680 |
| Intercept | | | | | |
| Downed wood | | | | | 8.67608 |
| *Mabuya varia* | 0.93 | 3 | 20.44 | 0.0179 | |
| Intercept | | | | | 5.85991 |
| Downed wood | | | | | −3.79646 |
| Termitaria | | | | | 22.76307 |

variable met the significance level for entry into the model for *Lygodactylus bradfieldi*. Other habitat variables (percent canopy cover, percent perennial grass) were not significantly associated with any lizard species in our analysis.

*Pedioplanis undata* was terrestrial in our study plots, while *Mabuya varia, M. striata,* and *Lygodactylus bradfieldi* were arboreal (including downed wood). A notable shift in microhabitat use from standing wood in open savanna to downed wood in bush-encroached habitat was observed in both *M. striata* and *L. bradfieldi*. In open savanna, 90% of *M. striata* observations and 100% of *L. bradfieldi* observations were made on standing wood. In contrast, only 17% of *M. striata* observations and 19% of *L. bradfieldi* observations in bush-encroached plots were on standing wood, despite a 42% increase in woody plant density in bush-encroached plots.

### 3.3. Arboreal lizard preferences to tree species and tree size classes

Habitat selection analyses indicated that arboreal lizards demonstrated a preference for only three tree species: *Acacia erioloba*, *A. fleckii*, and *A. reficiens* (Table 4). These species accounted for only 20% of all trees in our study plots, but 87% of all arboreal lizard observations. *Acacia erioloba* and *A. fleckii* were savanna species not found in bush-encroached areas, while *A. reficiens* occurred in both savanna and bush-encroached plots (but was more common in the savanna plots; $x=23.3$/ha in savanna vs. 11.7/ha in bush-encroached). Although *A. reficiens* occurred in all of our plots, lizards used this tree species primarily in bush-encroached plots (67% of observations in bush-encroached vs. 4% in savanna), where both *A. erioloba* and *A. fleckii* were absent. In contrast, invasive species such as *A. mellifera*, *A. tortillis*, and *Dichrostachys cinerea* comprised 56% of total woody plant composition yet only 9% of arboreal lizard observations were made from these species.

Lizards demonstrated a preference for trees greater than 3 m in height (Table 5). Over 53% of arboreal

Table 4
Selection indices for tree species as preference measures for arboreal lizard populations ($n = 128$ lizard observations)

| Species | Total woody spp. composition (proportion) | Number of lizard spp. observed | Proportion of arboreal lizard observations | Standardized Selection Index[a] |
|---|---|---|---|---|
| *Acacia erioloba* | 0.059 | 4 | 0.471 | 0.546 |
| *A. fleckii* | 0.074 | 4 | 0.269 | 0.249 |
| *A. reficiens* | 0.067 | 4 | 0.134 | 0.137 |
| *A. mellifera* | 0.130 | 2 | 0.025 | 0.013 |
| *A.hebeclada* | 0.074 | 2 | 0.025 | 0.023 |
| *A. tortillis/karroo* | 0.184 | 2 | 0.050 | 0.018 |
| *Dichrostrachys cinerea* | 0.243 | 1 | 0.017 | 0.005 |
| *Grewia* spp. | 0.068 | 1 | 0.008 | 0.008 |
| Other | 0.101 | 0 | 0 | 0 |

[a] Standardized selection indices above 0.11 indicate preferences.

Table 5
Selection indices for tree size-classes as preference measures for arboreal lizard populations ($n = 128$ lizard observations)

| Tree size-class | Proportion of total available trees | Proportion of arboreal lizard observations | Standardized Selection Index[a] |
|---|---|---|---|
| 1; 0–1 m | 0.521 | 0 | 0 |
| 2; 0–3 m | 0.458 | 0.461 | 0.039 |
| 3; >3 m | 0.021 | 0.539 | 0.962 |

[a] Standardized selection indices above 0.33 indicate preferences.

lizard observations were recorded for trees of this size class, which comprised only 2.1% of the total woody plant composition when averaged across habitat types. Although lizards did use woody plants between 1 and 3 m in height (46% of available trees), no lizard observations were made on woody plants less than one meter in height (52% of available trees; Table 5).

## 4. Discussion

We observed significant differences in the lizard assemblages between savanna and bush-encroached habitat types. Both *Pedioplanis undata* and *Lygodactylus bradfieldi* were, respectively, 3.9 and 2.7 times more abundant in savanna than bush-encroached plots. The assemblage differences, however, were primarily attributable to the absence of *M. varia* from all plots that were formerly savanna and a dramatic increase in the abundance of its congener, *M. striata*, which was 7.5 times more abundant in bush-encroached habitat than savanna. Differences were also observed among plots of the same habitat (Table 1) indicating that lizards are responding to microhabitat variables beyond the scope of this study. We detected lizard associations with certain quantified habitat variables but generalizations are difficult to surmise because of relatively low sample sizes and a lack of replicates.

*Mabuya striata* was the only species that experienced an increase in abundance in bush-encroached plots. It was also the only species surveyed that was regularly found on human-made structures in the area. The inflated population size of *M. striata* in bush-encroached plots could be a result of several factors including an increase in downed wood and/or possibly competitor release in the absence of *M. varia*. Similar trends have been reported for lizard assemblages in the south-western United States, where species abundance and diversity were generally lower in areas that were heavily grazed, with the exception of a few species that were positively affected by the change in vegetative structure concomitant with heavy grazing (Jones, 1981).

Arboreal lizards in our study were strongly associated with three particular tree species (*Acacia erioloba, A. fleckii,* and *A. reficiens*). These are non-invasive species associated with open savanna vegetation. They differ from the invasive species in that they have a flaky, loose bark structure that the arboreal lizard species utilized for cover. Cover provided by exfoliating bark also may support an extensive prey base of invertebrates. The invasive woody species in our plots (e.g. *Dichrostachys cinerea*, *Acacia tortillis*, and *A. mellifera*) are characterized by having smoother bark, which appears to offer limited small refugia for arboreal lizards. The apparent importance of this aspect of microhabitat structure is reinforced by our observations in bush-encroached areas, where arboreal lizards were observed primarily on downed trees—such dead trees develop similar loose bark as they decompose. In a study of *M. striata* habitat use in the Kalahari Desert region of Namibia, Cooper and Whiting (2000) also found this lizard to frequently use the tree *A. erioloba*, but could not demonstrate a statistical preference for this tree because it was by far the most common tree at their site. Similar to our study, Cooper and Whiting (2000) found a positive association between lizard abundance and tree size.

Limited diversity in habitat structure has also been posited for explaining reduced species richness in comparisons of lizard assemblages at similar latitudes (Pianka, 1986; Vitt, 1991; Vitt and Carvalho, 1995). Savanna plots in our study area were characterized by having relatively open grassy areas interspersed with mixed stands of woody plants. Bush-encroached plots lacked open grassy areas and were more homogenous in the spatial extent of woody plant cover (Fig. 1). Such increased structural homogeneity in bush-encroached plots may adversely affect lizard species diversity. There is little microhabitat separation between arboreal lizards among plots where all species frequent the same suite of tree species or, in the case of *L. bradfieldi* and *M. striata* in bush-encroached plots, downed wood. Such a low level of microhabitat segregation among species may be attributable to low structural diversity of microhabitats (Howard and Hailey, 1999).

There are several limitations to our study. Our sample sizes were small due to few replicate plots and apparent low lizard density. Therefore, generalizations about the effects of bush encroachment on lizard assemblages in southern Africa are limited. Although this study did not document the temporal processes of bush encroachment, we suggest that savanna plots more closely resemble ancestral savanna habitat, in both structural diversity and land-use history, than do the bush-encroached plots. Nevertheless, we suggest that controlled experimental manipulations be designed and implemented in order to better understand the effects of bush encroachment, habitat diversity, and native lizard assemblages.

In spite of these caveats, we did observe distinctions between bush-encroached and savanna lizard assemblages. In our study, one species (of only four predominant species in the area) disappeared and two species decreased in abundance with the shift in habitat. The native arboreal lizards do not use the invasive woody species, but shift to the patchy microhabitat of downed wood. Our study area was not subjected to extensive wood-gathering activity, but we are aware that downed wood is essentially absent from any area where humans rely on this resource for fuel. We expect that in bush-encroached areas utilized for fuel-wood, the lizard assemblage would be even more impacted.

The differences we documented between open savanna and bush-encroached plots are consistent with the trend of increasing bush density and decreasing structural diversity associated with human-mediated bush encroachment. The results of this study are congruent with studies of other taxa in the region. Our data suggest that large blocks of open savanna habitat are important in maintaining native lizard species diversity and relative abundance in Namibia. Human-mediated bush encroachment in southern Africa has been demonstrated to influence taxa as diverse as dung beetles, birds, small mammals, and diurnal lizards (Joubert and Ryan, 1999; Steenkamp and Chown, 1996; this study). Taken together, these results suggest a reorganization of the savanna ecosystem of southern Africa is underway, similar in scope to that recently documented by Brown et al. (1997) in semi-arid grasslands of North America.

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