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Structural and Animal Species Diversity in Arid and Semi-arid Savannas of the Southern Kalahari

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Abstract: The world is witnessing a decline in species diversity. In order to explore and preserve species diversity, ecologists still search for fundamental principles which may shape species diversity patterns in space and time. In arid and semi-arid savannas of the southern Kalahari in Southern Africa land use and climate change are two anthropogenic drivers which have a considerable impact on local animal species diversity. These drivers affect species diversity either directly or indirectly via changes in the 'structural diversity', i.e., vegetation-based landscape and habitat structures at relevant spatial scales. Here, we present an overview on empirical and modeling studies which focus on animal species diversity and response patterns of indicative species in the southern Kalahari. We show that land use forms such as wood cutting for charcoal and firewood production or shrub encroachment as a result of commercial cattle farming may have varying effects depending on the species or species group and the spatial scale that is considered. However, as a general conclusion we believe that land use in its present form is of particular concern and will have profound, mostly negative, consequences for animal diversity in the southern Kalahari. Furthermore, we provide several examples of how simulation models developed for indicative species may help to evaluate the possible impact of climate change as well as changes in structural diversity of the vegetation.

Key words: Biodiversity, climate change, keystone structure, land use, shrub encroachment, simulation models, spatial scale, structural diversity, wood cutting.

Savanna ecosystems cover approximately 20% of the earth's surface, and about 40% of Africa (Scholes and Walker, 1993). They are home to most of the human population of Africa and are the areas where population growth is most rapid (Scholes and Walker, 1993). In addition, they support a majority of African range lands, livestock and wild herbivore biomass (Scholes and Archer, 1997). In the southern portion of the Kalahari in South Africa where the Kalahari borders Namibia and Botswana, the vegetation structure mostly consists of large *Acacia* trees widely scattered within a landscape matrix of grassland, parallel sand dunes and dry river beds. Visitors appreciate this charming parkland character – it provides an image that is closely related to ancient roots of mankind when first societies of hunters and gatherers evolved. However, in the recent decades, human activity and land use expansion have resulted in substantial changes in this landscape

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Fig. 1. Typical landscape structure in the southern Kalahari: Acacia erioloba with nests of the sociable weaver (Philetairus socius). Large trees provide a keystone structure for a wide array of other plant and animal species.

structure, including the disappearance of the typical 'parkland' aspect provided by *Acacia* trees.

Recently, both empirical and modeling studies have revealed important insights into biodiversity patterns in the southern Kalahari. In order to summarize current knowledge, we present an overview on studies that focused on animal species diversity and 'structural diversity' in arid and semi-arid savannas of the southern Kalahari. The term 'structural diversity' used here refers to vegetation-based landscape and habitat structures at relevant spatial scales. In particular, we will aim on the impact of land use and climate change on the latter biodiversity components, as well as the direct link between structural and species diversity. For example, overgrazing as a result of commercial cattle farming, coupled with episodic droughts, has caused widespread rangeland degradation and loss of floristic and faunal diversity which, by current models, is unlikely to recover to 'climax' conditions even after a reduction in current stocking rates (Du Toit and Cumming, 1999). Due to the long time spans involved in these processes, population models of indicator species are a useful tool to study the impact of climate change and land use (see e.g., Wichmann *et al*., 2003). Since different animal species react differently to environmental changes, indicator species are unique environmental indicators offering a signal of the biological conditions of this ecosystem.

Introduction to the Ecology of South African Savanna

The typical vegetation structure of savannas in southern Africa, including the southern Kalahari, usually consists of large *Acacia* trees widely distributed in a grassy vegetation matrix (see Fig. 1). However, as for most ecosystems - at least from a human perspective - this typical savanna image is rather short-term because of long-term ecosystem dynamics affecting the landscape structure. In particular, the proportion between trees and grasses has shifted over the course of time, governed by major environmental drivers such as rainfall, fire, nutrients, herbivory and, of course, millennia of human activity.

Generally, water is the primary driver of the vegetation structure and ecological stability in savannas of southern Africa. The amount of rainfall determines grass biomass productivity, i.e., fuel load, and thus fire frequency, which in turn affects mortality and establishment of trees. A recent continental-scale analysis of study sites from Africa showed that in savannas, which receive less than 650 mm of rainfall annually, maximum woody cover is bounded by water availability (M. Sankaran, unpublished data). These arid and semi-arid savannas are potentially stable states where rainfall limits the predominance of trees and thus permits the coexistence of grasses and woody plants. Above this threshold, water availability appears sufficient for woody canopy closure. In other words, wet savannas are potentially unstable states where disturbances, such as fire or herbivory are required for maintaining the coexistence of both trees and grasses. In arid and semi-arid savannas, these disturbances govern the spatial distribution of woody plants within the relatively homogeneous grassland matrix. For example, both empirical and modeling studies showed that during wet periods trees tend to be spatially aggregated (because increased fire frequency decreases the probability of juvenile establishment in the open grassland), while in dryer periods the spatial pattern of rejuvenating trees changes to a more random pattern (e.g., Jeltsch *et al.*, 1999).

Human activity has resulted in major environmental changes in most parts of the southern Kalahari. In the southern Kalahari, the most momentous land use forms include commercial cattle farming and clear cutting of *Acacia* trees for charcoal and fire wood production. In recent decades, commercial harvest of camelthorn tree wood (*Acacia erioloba*) has resulted in severe changes of savanna vegetation structure (e.g., Anderson and Anderson, 2001). Land use in the form of commercial cattle farming has become a major threat to savanna integrity in most parts of the southern Kalahari. Overgrazing by cattle has led to an increase in woody shrub cover, a term called shrub encroachment. By consuming grass biomass cattle favor water availability for shrubs and trees, and reduce fire frequencies which in turn facilitate the establishment of woody plants. As a result of intra-sapling competition (Tainton and Walker, 1992), woody plants, however, remain small and ‘bushy’. Cattle also facilitate the establishment of fleshy-fruited, encroaching shrubs by dispersing their seeds into the open grassland (Tews *et al.*, 2004a). Besides land use practices, recent changes in climatic conditions effecting the amount and distribution of rainfall, may have important consequences for both structural and species diversity. Changes in the amount of rainfall have a direct effect on annual grass biomass productivity, fire regimes and tree establishment and, as a further corollary, other plant and animal species which depend on these resources.

In the southern Kalahari large, solitary trees function as a keystone structure, because they are focal points for animal activity (Tews *et al.*, 2004b). They supply nest sites, shade and scarce food resources. For example, ungulates need the sub-canopy of adult trees to rest in the shade; arboreal rodents utilize dead trees as a nesting site, or raptors and vultures use large, solitary trees as perches. Moreover, faeces and carcass remains left below the trees elevate levels of nutrients available to plants (Dean *et al.*, 1999). Thus, any change in the 'structural diversity' of the savanna vegetation, for example the removal of large, solitary trees for fire wood production, will have a direct effect on overall species diversity.

What is 'Structural Diversity' and How is it Effected by Land Use and Climate Change in the Southern Kalahari?

According to a basic definition of 'biodiversity' (UN Environmental Program, 1992) biological diversity means the variability among living organisms and the ecological complexes of which they are part. The biotic diversity of ecological complexes may comprize functional and spatial ecological structures. Biotic spatial structures may be formed by the terrestrial vegetation, for example by the canopy structure in a tropical rain forest or patchy distributed tree islands in the boreal forest-tundra ecotone. In this context, the term 'structural diversity' can be used to describe vegetation-based landscape and habitat structures at different spatial scales. Structural diversity may be applied to a wide array of spatial scales, ranging from the architectural structure of a single plant to community patterns in the vertical and horizontal plane or mosaic patches on a landscape scale. Both elements of biodiversity, i.e., 'species diversity' and 'structural diversity' are closely inter-linked and mutually maintain the integrity and function of an ecological system. If an external pressure is applied to one component, for example a key species or a crucial ecological structure, it will likely effect a cascade of linked elements and, in the long run, the whole biological system.

In arid and semi-arid savannas, such as the southern Kalahari, structural diversity is largely determined by woody vegetation. Both, solitary trees and shrub individuals or patches are key elements in an otherwise relatively homogenous landscape. Currently two different types of land use significantly change structural diversity in southern Kalahari savannas. Firstly, overgrazing by livestock may lead to shrub encroachment, i.e., the increase of unpalatable or less palatable woody vegetation combined with a decrease of herbaceous biomass production. This phenomenon is widespread throughout arid and semi-arid savannas of the world and is considered as one of the most threatening forms of range land degradation (e.g., Scholes and Walker, 1993; Jeltsch *et al.*, 1997). Secondly, fire wood cutting for commercial use, e.g., tree harvesting for charcoal production, has become a major threat for the typical savanna vegetation structure in many parts of the southern Kalahari. Increasing tourism and improved infrastructures lead to a profitable trade with fire wood cut in the Kalahari and sold in larger cities throughout the Western Cape and neighboring provinces (Raliselo, 2002).

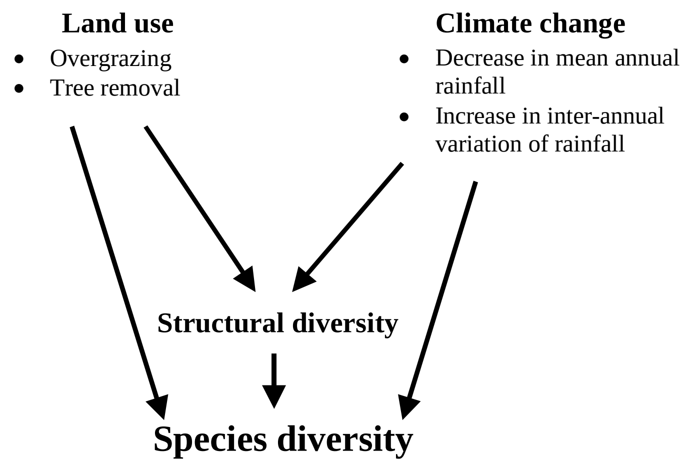

Fig. 2. Land use (e.g. cattle farming, wood cutting) and climatic changes influence species diversity, both directly and indirectly, via changes in the structural diversity (i.e. vegetation-based landscape and habitat structures).

In addition to land use, climatic changes may influence structural diversity in savannas. Changes in the tree/grass ratios of savannas have been primarily investigated in association with elevated CO_2 (Polley, 1997; Bond *et al.*, 2000). For example, Bond *et al.* (2000) suggested that higher rates of atmospheric CO_2 will have a positive effect on the post-fire regrowth of woody plants resulting in an increase in woody plant cover. However, it is likely that changes in precipitation as the key driving force in arid and semi-arid savannas will have more direct and profound effects. Changes in the precipitation pattern will directly influence establishment and mortality of trees as well as competition between herbaceous and woody vegetation (e.g., tree seedlings). In addition, precipitation changes will modify herbaceous biomass production and thus influence fuel production for grass fires. A decrease or increase of fire frequency and intensity, however, has been shown to significantly change tree pattern and density and thus structural diversity (Jeltsch *et al.*, 1999). Further possible, but yet hardly explored impacts of climatic changes on structural diversity in savannas include changes in dispersal processes of seeds by animals. This has been shown to be a crucial factor for tree pattern in the southern Kalahari (Jeltsch *et al.*, 1998). Another process that may turn out to be problematic under changed climatic conditions is the invasion of alien species, e.g., tree species from Australia in the Kalahari (Dean *et al.*, 2002).

Linking Structural and Animal Species Diversity

In the southern Kalahari land use and climate change may influence animal diversity directly as well as indirectly via changes in the structural diversity of the landscape (see Fig. 2). In the following we present a selection of empirical and modeling studies which show how different species groups and indicative species respond differently to changes in the structural diversity. Thereafter, we provide a more in-depth description on how variations in structural diversity at different spatial scales affect species diversity of rodents in the southern Kalahari.

Case examples of empirical studies linking structural and animal species diversity

Shrub encroachment as a result of overgrazing leads to a reduction of perennial grass cover. Hence, consumers depending on this resource may be negatively affected. A good example for this relationship are ground-dwelling, small rodents. The study of Meyer (2004) showed that in habitats with low perennial grass cover and a high proportion of bare ground and annual plants, habitat quality for small rodents strongly decreases due to a reduction in palatability. With the exception of *Desmodillus auricularis* (short tailed Gerbil), species diversity of ground-dwelling, small rodents were found to decrease with decrease in structural diversity and the presence of perennial grasses. Disturbed sites with a high cover of annual plants had the lowest species diversity (Meyer, 2004).

In contrast to ground-dwelling rodents, the black-tailed tree rat, *Thallomys nigricauda*, showed a different response pattern. This rodent is a widespread arboreal species occurring in many parts of the southern Kalahari. An increase of shrub density improves habitat conditions for the tree rat due to a better connectivity among suitable structures for food and mates (Eccard *et al.*, 2003). Leaves of *Acacia mellifera* and *A. luederitzii* comprize about 95% of the diet and thus shrub encroachment improves the food availability for the black tailed tree rat (see Meyer, 2004). However, for raising their offspring this species also needs large dead trees with caves and hollows for nesting. In some areas where dead trees are harvested for fire wood, suitable nesting trees might therefore become a limiting factor for the viability of local populations.

As for the black-tailed tree rat shrubby vegetation structures play an important role for the yellow mongoose, C*ynictis penicillata*, a small carnivore species in the southern Kalahari (Blaum, 2004). Interestingly, the effects of shrubs on this species are inconsistent across different spatial scales. Yellow mongooses were found to build their reproduction dens preferably under large shrub structures, which provide additional shelter against avian nest predators when raising the young. Moreover, long and sharp thorns of most shrub species, i.e., *Acacia mellifera*, effectively protect burrow systems from collapsing under hoof trampling. Whereas the impacts of larger shrub patches are positive at the micro-habitat scale, an increase in shrub density at larger spatial scales, i.e., home range areas, affects group size and reproduction success negatively. In his study, Blaum (2004) found that these indirect effects of shrub encroachment initially result in a decrease of prey abundance (i.e., rodents and insects) for the yellow mongooses.

Even though the black thorn, *Acacia mellifera*, provides an important food resource for the tree rat or shelter against predators for the yellow mongoose, it is nightmare for both farm and nature conservation management in the southern Kalahari. The recent transformation of previous open savanna towards black thorn thickets changed the composition of bird and mammal assemblages considerably (van der Walt and le Riche, 1999). In a recent study, Wasiolka (2003) investigated the relative influence of different black thorn shrub-densities on multiple species groups. Using three broad shrub cover categories (0%, 16% and 32%, respectively) he concluded that the species diversity of arthropods and reptiles was significantly lower on shrub encroached plots than on the other two categories. Different micro-habitat use of several species showed that a variety and sufficient quantity of structural elements such as grass tussocks, shrubs and open ground facilitate higher species diversity.

The latter results are similar to those of Meik *et al*. (2002) who studied the impact of shrub encroachment on terrestrial and arboreal lizard assemblages in open savanna. Arboreal lizards are associated with particular tree species, for example *Acacia erioloba*. These non-invasive species differ from invasive species by having a flaky, loose bark structure which arboreal lizard utilize for cover. Cover provided by exfoliating bark also may support an extensive prey base of invertebrates (Meik *et al.*, 2002). In contrast to woody species such as *Acacia erioloba*, the invasive woody species *Dichrostachys cinerea*, *Acacia tortillis* or *A. mellifera* are characterized by having smoother bark, which appears to offer limited small refugia for arboreal lizards and thus reduce their diversity. Endemic species, such as the Kalahari tree stink, *Mabuya spilogaster*, use *Acacia erioloba* trees as a keystone habitat and may be therefore extremely vulnerable towards anthropogenic perturbations (see Melzheimer, 2004).

Modeling studies on the impact of structural diversity on indicative species

Spatial simulation models may provide a useful tool for analyzing population persistence under specific settings of environmental conditions. It is widely accepted that space is a crucial model component (Jeltsch and Moloney, 2003), particularly when structural diversity is important in the life history of a species. In general, species respond differently to environmental change because of different adaptations to their environment (Erasmus *et al.*, 2002). As a consequence, single-species models focusing on indicative species may yield more knowledge on the impact of environmental perturbations than functional models which are based on theoretical groups of species with similar traits.

As in the case with the tree rat, the yellow mongoose (*Cynictits penicillata*) is a small carnivore species that is both negatively and positively affected by shrub encroachment. By using a spatial, individual-based simulation model, Popp (2004) found that total cover and, in particular, the spatial pattern of encroaching shrubs influenced the persistence of the yellow mongoose. A slight increase in shrub cover as a result of overgrazing may be of benefit for the yellow mongoose. However, if shrub density is increased beyond a certain threshold, population persistence is strongly decreased. Here, the range of persistence (in terms of shrub density) increased with increasing shrub patchiness. The results show that resource acquisition and predator avoidance via the structural diversity may have a considerable impact on population persistence.

In a study on the persistence of the tawny eagle (*Aqulia rapax*), a large raptor of southern Kalahari arid savanna, Wichmann *et al*. (2003) developed AQUIQUA, a stochastic computer simulation model. Based on their model, they found that very high, as well as very low tree densities can limit the persistence of the tawny eagle population, because this species needs large trees to build nests and open space for hunting. Moreover, they showed that deviations from a random tree distribution (i.e., clumped or evenly distributed) can shift these limiting tree densities. Even though the tawny eagle seems to be well adapted to this arid environment the above study provides evidence that changes in the structural diversity may have considerable impact on raptors with specific habitat requirements.

The sociable weaver (*Philetairus socius*) is a colonially living bird species that builds communal nests on *Acacias* and other trees. A field survey in the southern Kalahari revealed that nests are only built on trees with more than 100 cm trunk circumference, corresponding to an approximate tree age of 70 years (M. Schwager, unpublished data). In areas of low tree density or in bush encroached savannas with smaller woody plants, the availability of large nest trees might therefore limit the reproduction capability. Based on empirical data, a spatial explicit population model was used to investigate the effect of tree density and tree spatial pattern on population size and persistence of the sociable weaver (M. Schwager, unpublished data). Simulation results showed a limitation of colony density by tree density, however the limitation occurred only up to tree densities of about 10 tree per km^2, and population survival was still high at tree densities of about 0.5 trees per km^2. The high persistence of the population and the low limitation by tree density could be explained by the large home range and dispersal distance of the species, as well as by the colonial way of living, which allow the birds to live in high numbers on single trees, and build up a large (and persistent) population, even if trees are scarce. However, coupling the population model to a dynamic vegetation model (see Jeltsch *et al.*, 1996, 1998, 1999) under different woodcutting scenarios showed that, despite the high persistence, the population can be severely affected by the removal of solitary trees for charcoal and fire wood production. These results stress the high impact that woodcutting can have, especially in more arid areas with lower tree density.

The relevance of spatial scale for detecting species diversity patterns - A case example from the southern Kalahari

Organisms perceive habitat structures at different spatial scales (e.g., review in Tews *et al.*, 2004b). As a consequence, studying the impact of structural diversity on species diversity requires identification of the spatial scale at which species operate. A good example for the importance of spatial scale was shown by Blaum (2004) who studied rodent communities in the land use mosaic of the southern Kalahari. The land use pattern in the study area consists of differently stocked range lands with communal farming as well as areas currently used as game farms. This mosaic has led to a diverse spatial pattern of structural diversity at a regional scale, forming habitats of different quality. For rodents, single shrubs and shrub patches provide protection against avian predators as well as suitable nesting sites. Traveling within and between habitat patches is limited when shrubs or other dense vegetation cover are lacking. However, the proportion of grasses on total vegetation cover decreases with increasing shrub cover, resulting in a deterioration of food resources. Due to these varying effects of structural diversity Blaum (2004) investigated rodent diversity at two spatial scales: (1) a medium spatial scale of 1 ha equivalent to the mean home range size of rodents, and (2) a large spatial scale of 250 ha.

The results of this study show a unimodal response pattern of rodent diversity with increasing shrub cover. Maximum rodent diversity was found at a medium cover (12.5%) of shrubby vegetation. Surprisingly, this relationship was identified on a large spatial scale (250 ha) and not on the scale of the mean home range size (1 ha) of the study animals (Fig. 3). This contradicts previous results and other studies indicating the mean home range as the best predictive spatial scale for detecting patterns of species diversity (e.g., Schiegg, 2000). However, particularly in fragmented habitats, larger spatial scales become more important because gaps of resource-poor or unsuitable habitats limit habitat connectivity (Andren, 1994; Keitt *et al.*, 1997; Johnson *et al.*, 1992; Williams *et al.*, 2002; Crooks, 2002). Such resource gaps are major barriers across which an animal would have to travel to reach the neighboring patch for example, foraging, sheltering or nesting. Hence, the matrix of the landscape acts as a migration filter (Vandermeer and Carvajal, 2001). It is therefore essential to understand the effects of different spatial scales for different species groups and identify the corresponding spatial scale.

Modeling Studies on the Impact of Climate Change on Indicative Species

Climate change may have large and multiple effects in semi-arid and arid savannas of the southern Kalahari. The annual amount and variation in rainfall is particularly important for most plant and animal species and the ecosystem as a whole. Recent climate change studies propose a decrease in mean precipitation of 5-15% by the year 2050 (IPCC, 2001), as well as an increase in the frequency and variability of extreme rainfall events (e.g., Katz and Braun, 1992). It has also been hypothesized that alternating phases with low and high rainfall related to El Niño/La Niña phenomena may increase, i.e., future climatic conditions may be characterized by long drought periods followed by longer periods with above-average rainfall. Over larger time spans, these changes in rainfall will have profound effects for the local population persistence of different animal species via birth, dispersal and mortality processes.

To provide an example, results of a population model on the tawny eagle, *Aquila rapax*, (see Wichmann *et al.*, 2003) indicated an increase in the risk of extinction when climate changes as projected. Particularly, the long-term effects of decreasing mean annual rainfall may reduce population viability of the tawny eagle. Although the populations in the southern Kalahari are currently not threatened by extinction, a decrease in rainfall of 10% by the year 2050 will result in a survival time of the

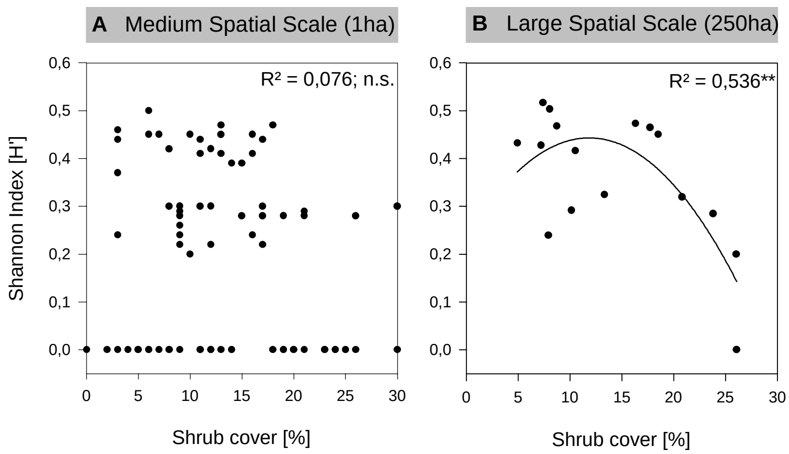

Fig. 3. Impact of increase in shrub cover on rodent diversity in the southern Kalahari for two spatial scales. The medium spatial scale is equivalent to the mean home range (A) and the large spatial scale represents the mosaic of land use patterns in the southern Kalahari (B). Only the large spatial scale indicates a significant response pattern (Blaum, 2004).

tawny eagle population of less than 100 years (Wichmann *et al.*, 2003, see also Wichmann *et al.*, 2004). For an increase in inter-annual variation of rainfall, however, even if mean rainfall amounts will remain unchanged, the population model predicts a severe decrease in the expected survival time (Wichmann *et al.*, 2003). The study showed that under the particular dry conditions in arid savannas, even top predators like the tawny eagle are affected by climate change.

In a modeling study of the colonially breeding sociable weaver *Philetairus socius*, M. Schwager (unpublished data) investigated the effect of changes in mean, variation and spatial pattern of rainfall on population dynamics of this species. Based on long term field data from the Kimberley area in the southern Kalahari (see Covas, 2002), the study showed that increasing variation of annual precipitation led to high population fluctuations. In large scale simulations, it was shown that the population might not only be affected by the temporal pattern, but also by the spatial pattern of rainfall. Due to the colonial way of living, the sociable weaver population can be seen as a metapopulation, for which a spatial correlation of environmental factors (rain) may lead to a synchronization of local population dynamics (Moran effect). As a consequence, simulations of an increased spatial autocorrelation of rain resulted in a decreased growth rate of the total population. Thus, since large nests of the sociable weaver are utilized by other birds, reptiles and mammals, local extinction may result in cascade effects for other species.

Conclusions

In this overview we showed how animal diversity in the southern Kalahari is affected by climate change and land use as well as via changes in the structural diversity of the vegetation. Based on the studies surveyed, there is increasing evidence that land use forms, such as wood cutting or cattle grazing, will have profound, mostly negative, consequences for animal diversity, since many species are adapted to the typical savanna vegetation structure. However, shrub encroachment may have both positive and negative effects depending on the species group and the spatial scale that is considered, as well as the severity of shrub encroachment. Moreover, based on empirical studies of species diversity of ground-dwelling rodents and small carnivores we highlighted the importance of the spatial scale in terms of the significance of the species diversity – structural diversity relationship. Furthermore, we provided several examples of how simulation models developed for indicative species help to evaluate the possible impact of changes in structural diversity and climate change, i.e., rainfall pattern. In particular, the proposed decrease in mean annual rainfall and increase in inter-annual variability may increase the extinction risk of particular species. However, as opposed to insights gained from modeling studies with a single species approach, large scale community effects of climate change are largely unknown. For example, such effects may include a zonal shift of species distribution, changes in functional mechanism of food webs or increasing invasion of alien species.

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