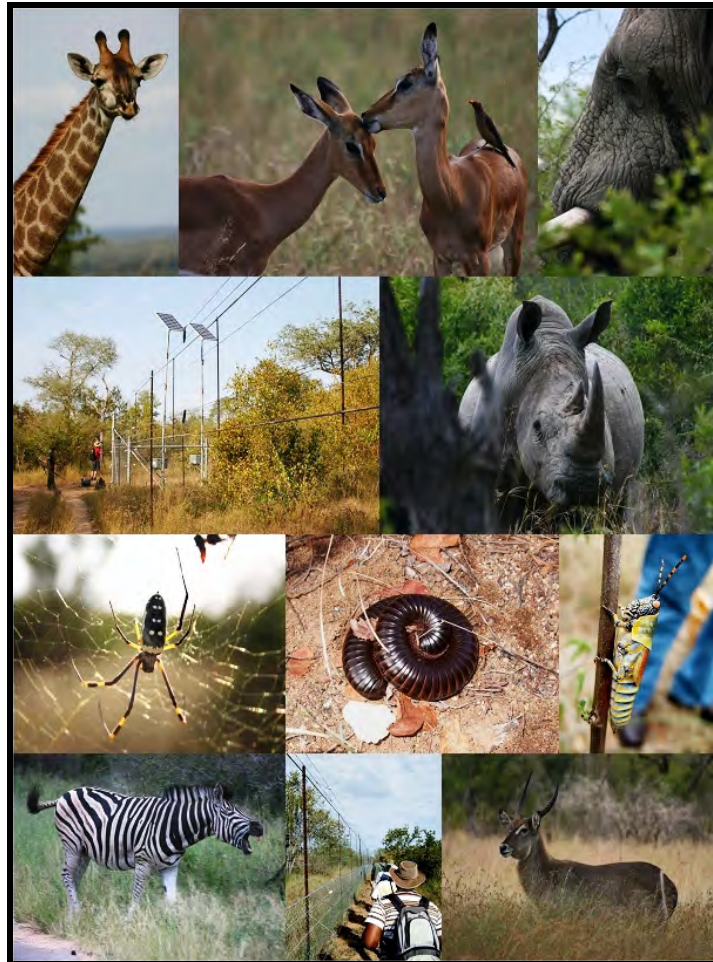

Indirect effects of mammalian herbivores on invertebrates in a river gradient of the Kruger National Park, South Africa

David Bell



Handledare: Joakim Hjältén and Micael Jonsson

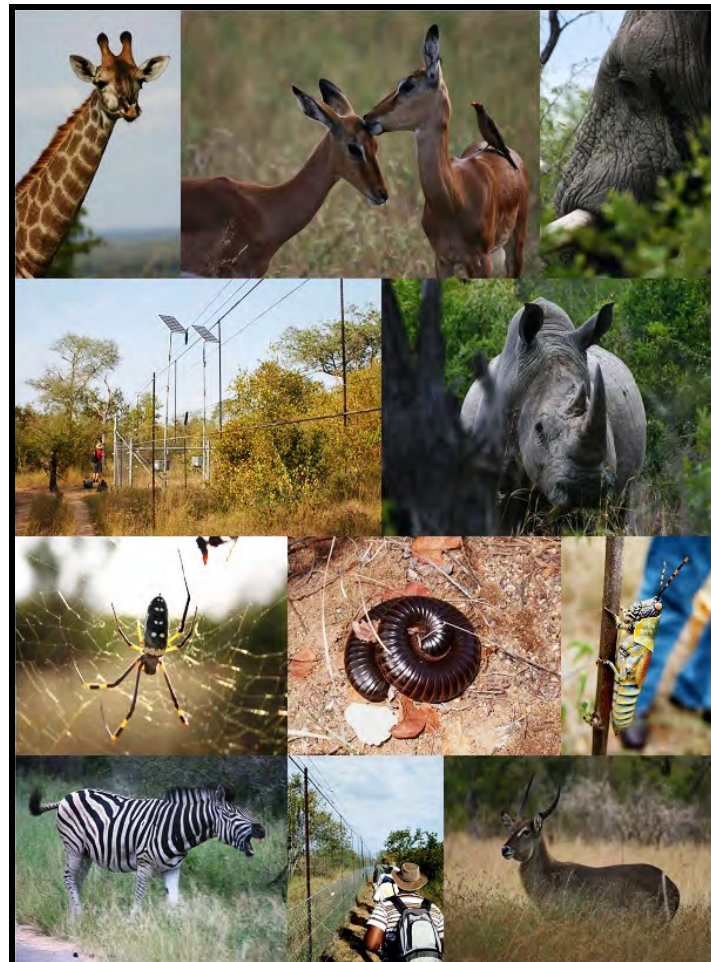
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Examensarbete i ämnet biologi

Indirect effects of mammalian herbivores on invertebrates in a river gradient of the Kruger National Park, South Africa

David Bell



Supervisors: Joakim Hjältén and Micael Jonsson

30 Point, D-Level

Abstract

Savanna biomes have been heavily affected by fire suppression, and changed grazing and browsing regimes, caused by human interventions. As a result many biotic interactions, and ecosystem functions, have been altered. Earlier studies have described extensive indirect effects of herbivores on invertebrates in arid systems that depend on arthropods for their nutrient recycling. Animals that feed on invertebrates might also be affected by changes in invertebrate abundance and composition. The aim of this study was to assess indirect effects of mammalian herbivores on invertebrates in a vegetational gradient towards a river. The initial questions were:

- Are there any differences in invertebrate richness and abundance along the catena, i.e. the vegetation gradient towards the river?
- Will the invertebrate richness and abundance change with different grazing and browsing pressures?

Invertebrate specimens were collected in three experimental sites, in three vegetation zones perpendicular to the Sabie River. The field work took place in March 2008, and resulted in information on the invertebrate richness and abundance. The results showed that large and medium-sized herbivores had effects on the invertebrate community, but also that the effects were site specific and different across invertebrate taxa. The river gradient had significant effects on the abundance of Araneae and Coleoptera, and the richness of Araneae and Formicidae. In general, the spider abundance and richness peaked at midrange from the river (in the foot slope). Coleopterans, on the other hand, were more abundant and taxon rich in the riparian zone. In addition to this, the riparian zone housed many ant taxa.

The experimental treatments had significant effects on the total abundance of invertebrates in the herbaceous layer, and on the abundance of Araneae, Coleoptera, Orthoptera and Formicidae. The total abundance was depressed by large mammalian herbivores, most likely by elephants, and medium-sized mammals affected the abundance and richness of Coleoptera and Orthoptera negatively. The results on spider abundance were inconsistent in the sense that large mammals only occasionally affected them negatively. Nevertheless, the results showed that invertebrates can be severely hit by changes in game abundance. Human induced changes of ungulate densities might, therefore, not only affect invertebrates at Nkuhlu, but also taxa and ecosystems elsewhere.

Introduction

In 1995, Scholtz and Chown listed 43,565 insect species; within 7,753 genera and 569 families, known to southern Africa. In reality there are probably twice as many insect species below the equator in Africa. According to Braack (2003) 40-60 percent of all insect species in South Africa inhabit the Kruger National Park (KNP). If that is the case, then approximately 50 percent of South Africa's insect species are conserved in an area less than one 20th the size of the whole country. The mixed knobthorn-marula woodlands, surrounding Skukuza in the southern parts of the KNP, are thought to provide living space for 2.4 metric tones of canopy-dwelling insects per square kilometre (in the warm and wet season), based on estimations made from fogging whole trees with pyrethrum knockdown insecticide (Braack 2003). These estimations exclude all other invertebrates, and insects below ground, in water, and in other plant tissues. Termites, grasshoppers and other non-canopy insects would most likely triple that figure. In comparison, the corresponding average mass for mammalian herbivores per square kilometre (impala and larger) is 2.3 metric tones (Braack 2003).

Due to their abundance, invertebrates play vital roles in ecosystems and occur at every level of the food chain. Among other things they alter the structure and fertility of soils, pollinate flowering plants, recycle nutrients and decompose organic materials (Seastedt et al. 1984, Greenslade 1992). Furthermore, they respond rapidly to environmental changes and might therefore be more suitable as indicator species than plants (Samways 1994). Spider diversity has, for instance, been found to be positively correlated with plant cover (Warui 2005). In 2005, Warui et al. found that spider communities can be used for biomonitoring of land use changes, as they are heavily and indirectly affected by grazing and browsing. They assumed that these indirect effects were caused by a reduction in plant biomass and habitat complexity, based on Wise (1993) that concluded that spider populations are limited by the availability of unique structural features in the habitat rather than by prey abundance.



Figure 1. One of many spiders in the KNP.

Previously, scientists have shown that the plant biomass (Lawton 1983), plant structural diversity (Allan et al. 1975, Lawton 1983) and plant species diversity (Murdoch et al. 1972, Siemann et al. 1998) can affect invertebrate richness and abundance. This is hardly surprising, since most invertebrates (approximately 75 percent) are phytophagous (Lawton et al. 1981). Nevertheless, other factors might also be important. For instance, changes in

microclimate and light regime, that in part are regulated by the plant community, might affect eurythermal and stenothermal species differently. Furthermore, detritivores might be influenced by nutritional fluxes and differences in litter availability (Tschardtke 1997, Suominen et al. 1999). Phytophagous invertebrates (Strong et al. 1984) might be influenced by changes in plant diversity as many of them have specialized diets.

Ungulates (grazers and browsers) might influence invertebrate communities both directly and indirectly by altering plant communities. Indirect effects follow when one organism changes the conditions for a second organism, and in turn affects a third part associated with the second. Indirect effects are typically examined in the context of trophic cascades, but are also considered when species compete for shared resources. Mammalian herbivores cause top-down effects on the vegetation (ungulate control of plant biomass), and in turn become “allogenic ecosystem engineers” that determine invertebrate densities by changing their physical environment and ecosystem functioning (Jones et al. 1994 & 1997). Hence, this chain of interactions involves both top-down and bottom-up effects (resource control of invertebrate densities).

Jones et al. (1997) anticipated that physical ecosystem engineers would benefit biodiversity and invertebrate abundances at large spatial scales. An example of this would be the African elephant which is best known for its role in maintaining open wooded grasslands (savannas) by reducing habitat complexity (Laws 1970, Dublin et al. 1990). However, many herbivores native to Africa are declining because of habitat destruction, disease, poaching and competition with cattle (du Toit et al. 1999, Ottichilo et al. 2000, Georgiadis et al. 2003), and the consequences of these declines for many plants and animals remain relatively unknown.



Figure 2. Feeding elephants.

The disappearance of mammalian herbivores might severely alter ecosystems of today. In the late Pleistocene the elimination of megaherbivores caused vegetation changes that in turn caused the extinction of half of the mammalian genera (Owen-Smith 1987). However, it is not certain that invertebrates will be negatively affected by ungulate declines. Previously, scientists have reported positive (Abensperg-Traun et al. 1996, Ellingsen et al. 1997, Seymour et al. 1999, Suominen et al. 1999), negative (Dennis et al. 1997, Strand et al. 1999, Suominen et al. 1999), and neutral responses (Rambo et al. 1999) among invertebrates to grazing and browsing by large herbivores. According to Milchunas et al.

(1988) the response of a community to grazing depends on its evolutionary history. For instance, in communities adapted to moderate grazing both very high and very low grazing pressures can be regarded as disturbances. Hence, most plants and invertebrates of the African savanna are likely to be equipped with adaptations enabling them to survive intermediate grazing and browsing pressures.



Figure 3. Plant defence (spines) against browsing.

At the level of an individual tree it has been shown that phytophagous insects are more numerous in browsed deciduous trees, than in trees spared from mammalian herbivory (Danell et al. 1985, Roininen et al. 1997, Martinsen et al. 1998). On the other hand, Pringle et al. (2007) associated an herbivore induced increase in tree density and profile complexity with an increase in lizard and beetle density. Furthermore, they showed that the strength of the indirect effects was negatively correlated with productivity, with the exclusion of megaherbivores generating greater indirect effects in less productive sites. Hence, a low primary production (caused by low annual rainfall or reduced soil nutrients) might make an ecosystem less resilient to high grazing and browsing pressures. To explain the results, Pringle et al. (2007) argued that the compensatory re-growth of plants was faster in productive sites. An alternative explanation was that plants vary in edibility along a resource gradient. Pringle spoke in favour of the first assumption, but could not reject the latter possibility since certain acacia trees (*Acacia drepanolobium*) suffered lower rates of browsing by elephants on productive soils. This does of course insinuate that trees afford more elaborate defences where nutrients are plentiful.

This report will account for the indirect effects of herbivores on invertebrates in a gradient towards the Sabie River. Rivers deposit large amounts of nutrients in riparian zones, but water is also accessible throughout the lean season in riparian zones. Herbivores tend to favour riparian zones where food and water is plentiful, and in turn deposit nutrients there in the form of dung. This is not to say that other factors are not important. River floods might, for instance, create new succession orders that favour biodiversity by eradicating competitive plants (Chopin et al. 2007). African savannas are characterized by distinct wet and dry seasons, with fluctuations in food availability for herbivores. The amount and distribution of rain water throughout the wet season determines the survival of key dietary components into the lean season. In the dry season, grazers move towards the river in search of lush vegetation, only to return when short nutritional grasses are plentiful

elsewhere (Bell 1971). Browsers, e.g. giraffes (Pellew 1984), kudus, impalas and elephants (Stokke et al. 2002), also shift up and down the catenary drainage gradient between seasons. Consequently, both grazers and browsers congregate in riparian zones during the dry season in search of food and drinking water.

Although all herbivores deposit nutrients (dung), it is not certain that grazers and browsers influence the nutrient cycling in the same way. It is well established that grazers maintain their habitat by enabling fast nutrient cycles. Two reasons being: intense grazing during the growing season, and retention of nutrients close to the surface of the soil (McNaughton 1979, 1984, McNaughton et al. 1988). It has been heavily debated whether or not a similar positive feedback loop (browsing – regrowth – rebrowsing) occurs between ungulates and Acacia trees in the KNP. No convincing results have been presented for Acacia trees and browsers in Africa, but in North America evidence show that browsers influence nutrient cycles in an opposite way to that of grazers. For instance, selective browsing by moose favours slow-growing and unpalatable woody plants with slowly decaying litter – making previously attractive areas unappealing to browsers (Bryant et al. 1991, Pastor et al. 1993).

In exclosures free from browsers the litter production, relative humidity, and soil moisture might be higher than in browsed plots. Consequently, browsed plots might have higher light intensities and soil temperatures (Kielland et al. 1998). North American moose affect leaf litter quality and quantity along with canopy openness, and in turn the magnitude and direction of both direct and indirect effects. Experiments with invertebrates living on the forest floor also support this thesis. Suominen et al. (1999) did, for instance, confirm higher insect abundances in browsed plots (beetles within the family Curculionidae being the only exception). Hence, browsers can influence the flora and fauna at ground level via indirect effects on the habitat quality.

Better understanding of browser-induced changes in the vegetation, and in turn their indirect effects on invertebrates, is necessary given that human populations and their domestic animals are on the rise (Scholes 1997, Scholes et al. 1997). Savanna biomes are of great socio-economic importance and have already been heavily affected by fire suppression and altered grazing regimes (Scholes et al. 1997). Previously, many papers have described extensive indirect effects (negative and positive) on invertebrates in arid systems (Seymore et al. 1999, Gomez et al. 2002, Warui et al. 2005). This is increasingly worrying, since arid areas are dependent on macroinvertebrates for their nutrient recycling when fires are suppressed (Holt et al. 1990). Furthermore, animals feeding on invertebrates might be indirectly affected by grazing and browsing if abundances and species compositions change.



Figure 4. Animals that feed on invertebrates. Photo (lizard): Micael Jonsson.

With the knowledge gaps and herbivore declines in mind, further investigations of the indirect effects of herbivores (grazers and browsers) on invertebrates in the lower catena seem relevant. Furthermore, comparisons between riparian and other vegetation zones appear appropriate. In addition, different ungulates might affect invertebrates in different ways, both directly and indirectly. For instance, elephants, by being large consumers of plant biomass, might affect the diversity and abundance of invertebrates in a greater way than other herbivores. Much of the literature does in fact revolve around the concern that elephants in abundance (in protected areas like the KNP) will cause habitat degradation (Caughley 1976, van Aarde et al. 2007).

In order to investigate the indirect effects of herbivores on invertebrates in a catena, experiments were conducted in two exclosures (the Nkuhlu exclosures of Skukuza), in close proximity to the Sabie River, in the KNP of South Africa. The invertebrate richness and abundance were estimated in three vegetation zones of both exclosures, at different distances from the river. One exclosure allowed no herbivores (>15 kg) to enter, while the other one prevented only elephants and giraffes. The area in between the two experimental sites acted as a control.

The initial questions were:

- Are there any differences in invertebrate richness and abundance along the catena, i.e. the vegetation gradient towards the river?
- Will the invertebrate richness and abundance change with different grazing and browsing pressures?

In other words, can the river gradient and the different grazing and browsing pressures influence the strength of indirect effects of herbivores on invertebrates?

Methods

Study system

The Nkuhlu exclosures are situated on sandy (granite) soils, in close proximity to the Sabie River, in the Kruger National Park of South Africa. The Kruger National Park (KNP) covers both tropical and semi-tropical arid lands, with summer rainfalls in November until March. The mean amount of rainfall is 530 mm, and summers are hot with mean temperatures of 26.3°C. Winters are often very mild, and frost is unusual.



Figure 5. The Kruger National Park (in red) of South Africa.

The exclosures are approximately 50 ha (1.0 x 0.5 km) in size, and are separated by an unfenced distance of 400 meters (control area). Both exclosures extend topographically towards the river, and enclose an array of thickets and soils that characterize the region. The electric wiring in the full exclosure hinders all large herbivores (> 15 kg) from entering. The two electric cables (at 1.8 and 2.2 meters) in the partial exclosure only deter elephants and giraffes. Electricity in both cases is provided by solar panels. Both exclosures were erected in 2002.



Figure 6. The full exclosure.



Figure 7. The partial enclosure.

The ungulate fauna includes impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardus*), elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), waterbuck (*Kobus ellipsiprymnus*), reedbuck (*Redunca fulvorufula*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchellii*), buffalo (*Syncerus caffer*) and duiker (*Sylvicapra grimmia*).

Study methods

The field work took place in March 2008 and lasted for four consecutive days (the 18th to the 21st). Earlier three vegetation zones had been identified in a gradient towards the river:

1. The crest (Combretum-Sclerocarya association),
2. Foot slope (sodic area), and
3. Riparian zone (riparian and in-stream community).



Figure 8. The vegetation zones of Nkuhlu (Photo: O’Keefe and Alard 2002).

Within each vegetation zone of every treatment (control, partial and full enclosure), seven 0.3 litre pitfall traps were positioned ten metres from a randomly chosen coordinate. The pitfall traps were filled with approximately 0.1 litre of water-glycol mixture (50:50) and a small amount of detergent, in order to preserve the caught invertebrates. The pitfall traps were never placed directly under trees to avoid effects of tree proximity on the invertebrates, and since the soil at times could be impossible to penetrate. The pitfall traps were dug into the ground in early morning, and collected two days later (also in the morning). Sweep-net samples were also collected at the same sites as those used for pitfall trapping. Five sweeps equalled one sample, and the procedure was repeated five times at each site (always by the same person). The sampling was restricted to areas with vegetation, and the exact locations therefore had to be selected in the field. In total, 45 sweep-net samples were collected.

To begin with, all invertebrates were divided into broad taxonomic groups (class/order). The dominant taxonomic groups (Araneae, Orthoptera, Coleoptera and Formicidae) were then looked at separately, so that the family and/or genus of each specimen could be determined. Last but not least, the coleopterans were divided into morphotypes based on their morphological features. However, this project did not aim at investigating any particular species. Instead the main objective was to collect information on general invertebrate abundance and taxonomic composition (taxon richness; classes, orders, families and genera).

Statistical methods

The effects of the experimental treatments and the river gradient on the invertebrate community were analysed by using ANOVA in R. If necessary, to achieve normal distribution, the data was transformed. If *log* and *square root* transformations failed, a non-parametric test was run its place. At this point, collected values were given a rank, only to be reanalysed in an alternative ANOVA. Unfortunately, non-parametric tests of this kind can not estimate interaction terms. In all cases, the null hypothesis was rejected at $P = 0.05$. TukeyHSD tests were used for the pair-wise comparisons of the treatments (control, partial and full enclosure) and vegetation zones (crest, foot slope and riparian zone).

Results

Total abundance and richness

Sweep nets

The analysis on total abundance revealed a significant treatment term (Table 1), and the post-hoc analysis confirmed that the partial and full enclosure differed from the control ($P = 0.018$ and $P = 0.008$, respectively). In general, the invertebrates were more abundant in the partial and full enclosure than in the control (Fig. 9).

The ANOVA revealed no significant effects of the experimental treatments or the vegetation zones on the invertebrate richness, although the treatment effect on the taxon richness was close to significant (Table 1). The largest difference in taxon richness was found in the crest, where the total taxon richness was greater in the control than in the full enclosure (Fig. 10).

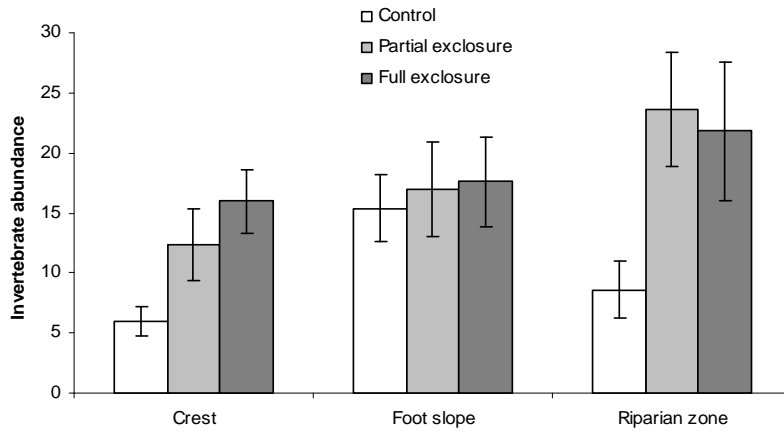


Figure 9. The invertebrate abundance (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial exclosure and full exclosure).

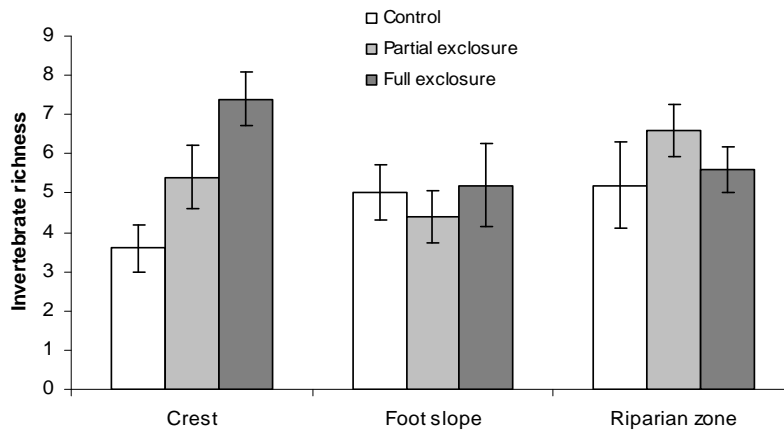


Figure 10. The invertebrate taxon richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial exclosure and full exclosure). Taxon richness in classes (Chilopoda, Diplopoda and Gastropoda) and orders (Arachnida and Insecta).

Table 1. ANOVA and non-parametric test results on the invertebrate richness and abundance. Significant ($P \leq 0.05$) a posteriori comparisons are denoted by \neq . Treatments; C = control, PE = partial enclosure, and FE = full enclosure. Vegetation zones; CR = crest, FS = foot slope, and RZ = riparian zone.

Abundance	Factor	df	MS	F	P	A posteriori comparisons
Total (sweep nets)						
ANOVA	Treatment	2	5.972	6.143	0.005	C \neq FE, C \neq PE
	Vegetation zone	2	2.829	2.910	0.067	
	Treatment & Vegetation zone	4	1.292	1.329	0.278	
	Error	36	0.972			
Araneae						
ANOVA	Treatment	2	1.367	4.578	0.017	C \neq PE, FE \neq PE CR \neq FS
	Vegetation zone	2	1.214	4.067	0.026	
	Treatment & Vegetation zone	4	0.498	1.667	0.179	
	Error	36	0.299			
Coleoptera						
Non-parametric	Treatment	2	1099.2	10.006	< 0.001	C \neq FE, FE \neq PE CR \neq RZ
	Vegetation zone	2	497.9	4.531	0.017	
	Error	40	109.9			
Orthoptera						
Non-parametric	Treatment	2	1233.1	10.903	< 0.001	C \neq FE
	Vegetation zone	2	300.1	2.653	0.083	
	Error	40	113.1			
Total (pitfall traps)						
Non-parametric	Treatment	2	1095.2	3.477	0.037	C \neq PE
	Vegetation zone	2	187.2	0.594	0.555	
	Error	58	315			
Richness	Factor	df	MS	F	P	A posteriori comparisons
Total (sweep nets)						
ANOVA	Treatment	2	0.367	2.840	0.072	
	Vegetation zone	2	0.118	0.914	0.410	
	Treatment & Vegetation zone	4	0.260	2.013	0.113	
	Error	36	0.129			
Araneae						
Non-parametric	Treatment	2	64.9	0.453	0.639	CR \neq FS, FS \neq RZ
	Vegetation zone	2	868.5	6.070	0.005	
	Error	40	143.1			
Coleoptera						
Non-parametric	Treatment	2	1195.4	10.376	< 0.001	C \neq FE, FE \neq PE
	Vegetation zone	2	295.4	2.564	0.090	
	Error	40	115.2			
Orthoptera						
Non-parametric	Treatment	2	1933.4	22.968	< 0.001	C \neq FE, C \neq PE, FE \neq PE
	Vegetation zone	2	178.1	2.115	0.1339	
	Error	40	84.2			
Araneae + Coleoptera + Orthoptera						
ANOVA	Treatment	2	4.022	0.943	0.399	CR \neq FS
	Vegetation zone	2	17.422	4.083	0.025	
	Treatment & Vegetation zone	4	5.622	1.318	0.282	
	Error	36	4.267			
Total (pitfall traps)						
ANOVA	Treatment	2	0.005	0.046	0.955	
	Vegetation zone	2	0.223	1.886	0.162	
	Treatment & Vegetation zone	4	0.092	0.774	0.547	
	Error	54	0.1184			
Formicidae						
Non-parametric	Treatment	2	458.0	1.659	0.199	FS \neq RZ
	Vegetation zone	2	1949.6	7.060	0.002	
	Error	58	276.2			

Pitfall traps

The pitfall traps caught mainly ants, and the results on total abundance and ant abundance were therefore very similar. The non-parametric test generated a significant treatment term (Table 1), and the post-hoc analysis revealed a difference in abundance between the control and partial exclosure ($P = 0.044$). A close to significant treatment ($P = 0.054$) and interaction ($P = 0.061$) term in an initial ANOVA made further investigations of the interaction term desirable, but the non-parametric test's inability to handle interaction terms made such investigations impossible. However, the total abundance appeared to be declining towards the river in the partial exclosure, whereas the opposite pattern appeared to be true for the control and full exclosure (Fig. 11). No differences in total taxon richness were identified between the experimental treatments in the catena (Table 1, Fig. 12).

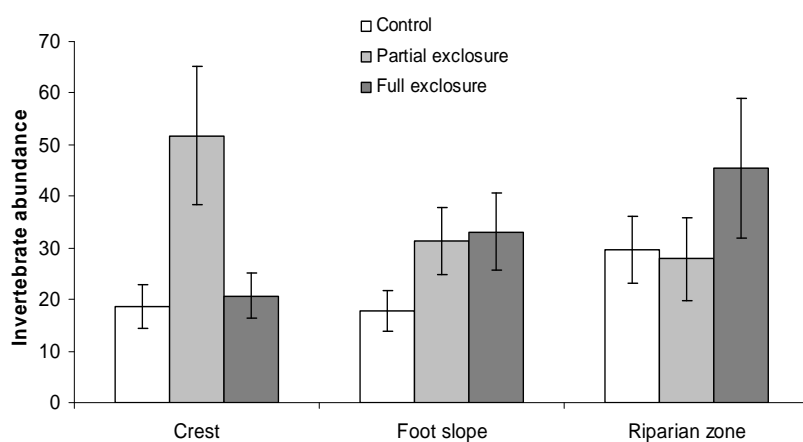


Figure 11. The invertebrate abundance (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial exclosure and full exclosure).

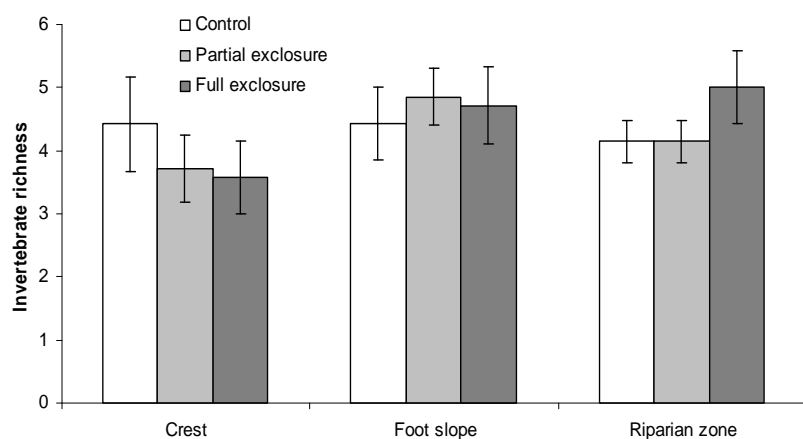


Figure 12. The invertebrate taxon richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial exclosure and full exclosure). Taxon richness in classes (Chilopoda, Crustacea and Diplopoda) and orders (Arachnida and Insecta).

Formicidae, Araneae, Orthoptera and Coleoptera in depth

The sweep-net sampling revealed that the dominant orders in the undergrowth were Araneae, Orthoptera and Coleoptera. Their counterpart in the pitfall traps was Formicidae

(Hymenoptera). The results have thus far dealt with the total invertebrate richness and abundance for each sampling method. Here, results on four orders will be presented in further detail. The families within Araneae, Orthoptera and Coleoptera will also be combined to give a better estimate on total richness.

Formicidae

The outcome of the ant abundance analysis has already been covered, which leaves us with the ant richness analysis. According to the non-parametric test, ant richness was affected by the river gradient (Table 1), and the post-hoc analysis revealed differences between the riparian zone and the foot slope ($P = 0.001$). The ants were more taxon rich in the riparian zone than in the foot slope, except for in the control of the foot slope where ant richness was much higher than in the partial and full enclosure (Fig. 13).

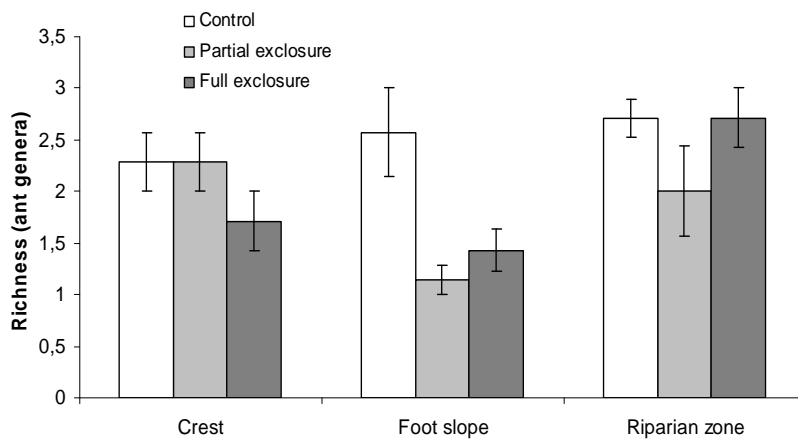


Figure 13. The ant genera richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial enclosure and full enclosure).

Araneae

The ANOVA on spider abundance revealed significant effects of the experimental treatments and the river gradient (Table 1), although the differences in abundance only were apparent in the riparian zone (Fig. 14). The post-hoc analysis showed significant differences between the control and partial enclosure ($P = 0.04$), but also between the partial and full enclosure ($P = 0.028$). The post-hoc analysis also revealed that the crest and foot slope were significantly different from each other ($P = 0.026$). The sweep nets caught plenty of spiders, and only one sample failed to obtain any specimens. The overall abundance was higher in the foot slope than in the crest, with one exception being that the spiders remained abundant towards the river in the partial enclosure (Fig. 14).

The non-parametric test showed that the spider genera richness was influenced by the river gradient (Table 1). The post-hoc test revealed that the foot slope was significantly richer in spiders than the crest and riparian zone ($P = 0.005$ and $P = 0.049$, respectively). The effects of the vegetation zones on spider richness were not as clearly expressed in all treatments, especially not in the full enclosure (Fig. 15). In addition to this, no clear difference was found between the foot slope and the riparian zone in the partial enclosure. The differences in spider genera richness between the vegetation zones of the control were, however, in accordance with the results from the post-hoc test (Fig. 15).

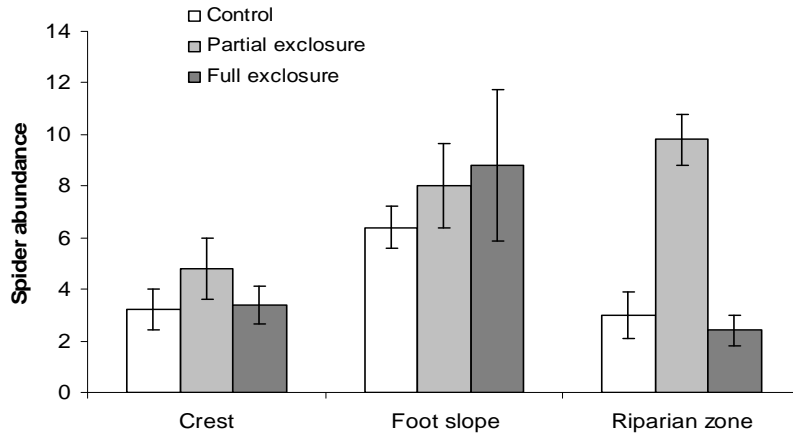


Figure 14. The spider abundance (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial exclosure and full exclosure).

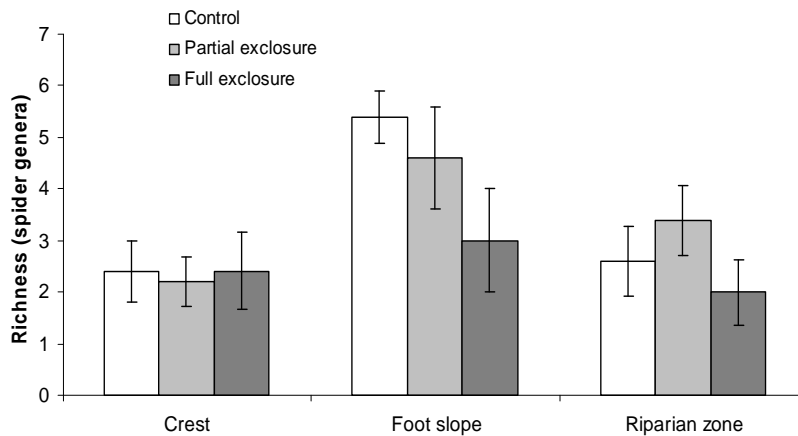


Figure 15. The spider genera richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial exclosure and full exclosure).

Orthoptera

The non-parametric test confirmed that the orthopteran abundance was influenced by the experimental treatments (Table 1). The post-hoc analysis revealed a significant difference between the control and full exclosure ($P < 0.001$). Furthermore, the differences in abundance between the exclosures ($P = 0.062$), and between the control and partial exclosure ($P = 0.062$), were only marginally significant. Also the vegetation zones in the catena showed differences in abundance that were close to significant (Table 1). The orthopterans were seemingly less abundant in the crest and riparian zone of the control than in the corresponding vegetation zones of the full exclosure (Fig. 16). The largest observable difference in overall abundance between the vegetation zones was found between the crest and the foot slope, where the orthopterans were more abundant in the foot slope than in the crest.

An additional non-parametric test proved that the experimental treatments also affected the orthopteran family richness (Table 1). In general the orthopteran richness was greater in the absence of the medium-sized ($P < 0.001$) and/or large herbivores ($P < 0.001$). The post-hoc test also revealed a difference in orthopteran richness between the partial and full exclosure ($P = 0.021$). The treatment effect was most apparent in the crest and riparian zone (Fig. 17). Medium-sized herbivores appeared to have general effects irrespective of the vegetation zone, while large herbivores appeared to be less important in the crest.

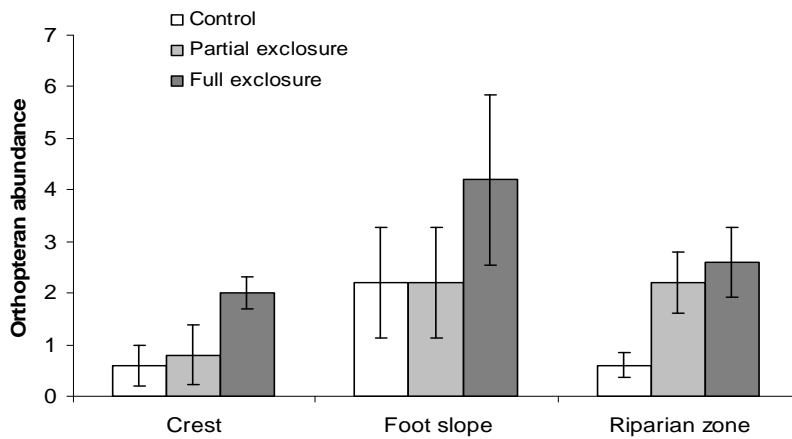


Figure 16. The orthopteran abundance (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial enclosure and full enclosure).

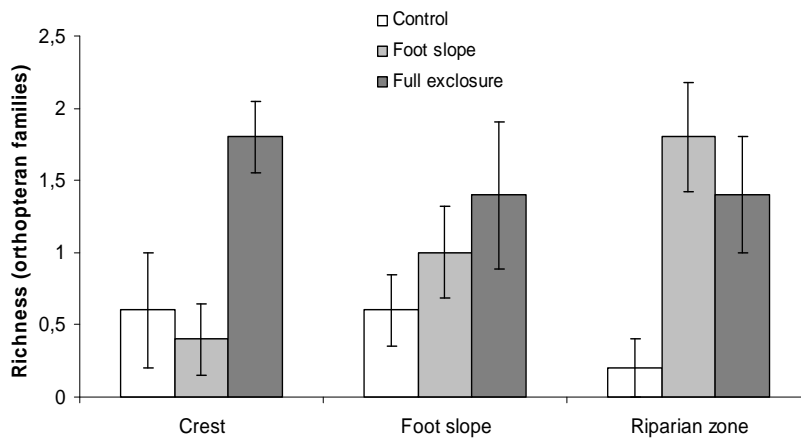


Figure 17. The orthopteran family richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial enclosure and full enclosure).

Coleoptera

Although the beetles were sparsely distributed, the results showed that the coleopteran abundance was affected by the experimental treatments and the river gradient (Table 1). The post-hoc analysis revealed specific differences between the partial and full enclosure, and between the full enclosure and the control ($P = 0.039$ and $P < 0.001$, respectively). In the catena, the crest differed from the riparian zone ($P = 0.014$). The beetles were more abundant in the full enclosure, but seemingly only in the crest and riparian zone (Fig. 18). Furthermore, there were differences in abundance across the vegetation zones of the catena.

Less than 60 percent of all samples contained coleopterans. Nevertheless, the non-parametric test revealed a significant treatment effect, and a close to significant catena effect, on the coleopteran family richness (Table 1). The post-hoc test revealed significant differences between the enclosures ($P = 0.016$), and between the control and full enclosure ($P < 0.001$). The variation in coleopteran richness was large (Fig. 19). No differences in coleopteran family richness were visible in the crest and foot slope between the experimental treatments, but the results from the post-hoc test were clearly reflected in the riparian zone, in which the beetles were more diverse in the full enclosure. The only

difference in richness that could be distinguished between the vegetation zones of the river gradient was that between the crest and riparian zone in the full enclosure. The results were almost identical for the morpho-species within the order Coleoptera as they rarely outnumbered the number of families (no figure presented).

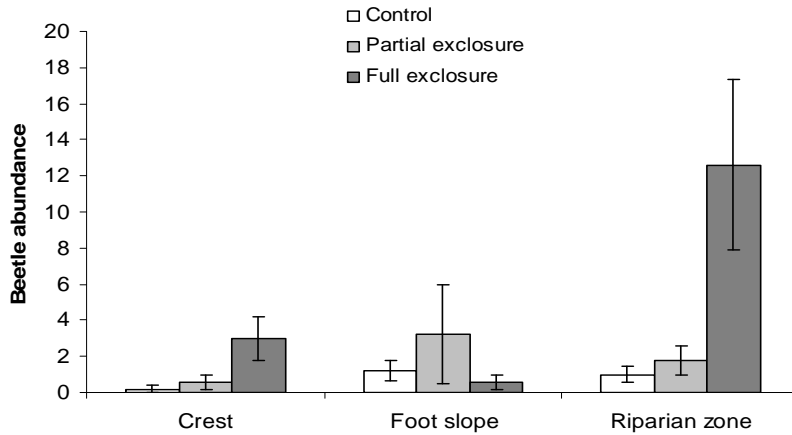


Figure 18. The beetle abundance (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial enclosure and full enclosure).

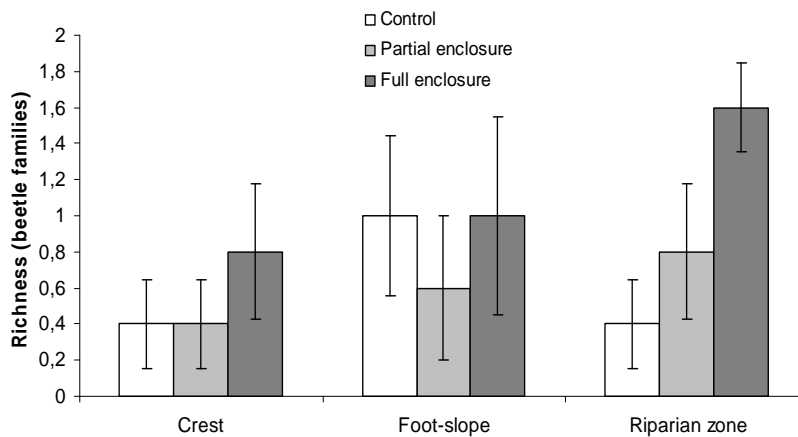


Figure 19. The beetle family richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial enclosure and full enclosure).

Araneae, Orthoptera and Coleoptera combined

Time limitations meant that only the most numerous orders could be divided into families. The analysis on the combined taxon richness for Araneae, Orthoptera and Coleoptera did, however, render a significant result (no significant differences were revealed in the analysis on total richness). The ANOVA showed differences across the vegetation zones of the catena (Table 1). That is, between the foot slope and the crest ($P = 0.02$) according to post-hoc analysis. The foot slope was more taxon rich than the crest, but only in the control and partial enclosure (Fig. 20).

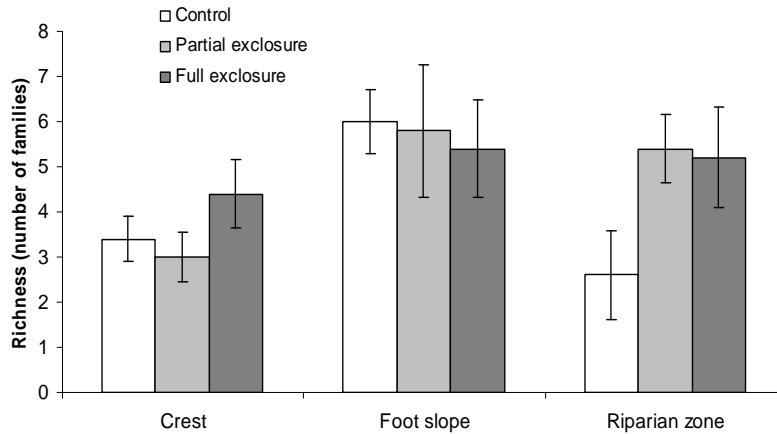


Figure 20. The spider, beetle and orthopteran family richness (mean \pm 1 SE) in the vegetation zones (crest, foot slope and riparian zone) of each treatment (control, partial enclosure and full enclosure).

Discussion

Are there any differences in invertebrate richness and abundance along the catena?

This study supports the assumption that invertebrate communities change in composition towards rivers. No general conclusions could be made for the entire invertebrate community at Nkuhlu, but many results showed that certain taxonomic groups, e.g. Araneae, Coleoptera and Formicidae, were affected by the conditions set by the river gradient. One determinant ought to be the productivity, since areas in close proximity to rivers are expected to be more productive. Beforehand I had expected to find differences in both richness and abundance along the river gradient, but on many occasions only one measurement was affected. The river gradient did, for instance, only affect the ant richness, as opposed to both the ant richness and abundance. There are, however, many other factors than productivity that can influence the richness and abundance of invertebrates, e.g. the plant biomass (Lawton 1983), plant species diversity (Murdoch et al. 1972, Siemann et al. 1998) and plant structural diversity (Allan et al. 1975, Lawton 1983).

Plant biomass appeared to be of great importance for the beetles at Nkuhlu, since most of the beetles were captured in the rich (large plant biomass) riparian zone. The orthopterans did not show the same dependence, since they were not affected by the river gradient, although the effect was close to significant. Perhaps the orthopterans were more mobile and therefore less habitat specific than the beetles? The spiders were significantly more abundant and species rich in the foot slope where the vegetation was scarce. This was quite surprising, since spiders usually respond positively to increases in plant biomass and structural complexity (Warui et al. 2005). The sweep sampling, however, was only conducted in areas with vegetation, and sodic areas had less vegetation cover. This might have confounding effects on the results, since a per ha measure might produce an opposite pattern. Thus, I can not argue that spiders are more abundant or taxon rich in the foot slope.

Sometimes indirect effects of herbivores on invertebrates were equal in strength, if not stronger, in the riparian zone (productive area) of Nkuhlu (see Fig. 9, 16, 17, 18 and 19). The results from Nkuhlu contradict Pringles (2007) theory on weaker indirect effects in productive areas, but the contradictions can potentially be explained by higher densities of

mammalian herbivores in the riparian zone. Warui et al. (2005) did, for instance, show that cattle can have stronger indirect effects on spiders than native herbivores, but only if they are more numerous. Mammalian ungulates might congregate in the riparian zone for many reasons, e.g. the quantity, quality and diversity of foods, and the closeness to drinking water, and thereby have strong effects on the vegetation, and subsequently on the invertebrates, despite high productivity.

Will the invertebrate richness and abundance change with the different grazing and browsing pressures?

In general, the results from Nkuhlu showed that the mammalian herbivores influenced the invertebrate abundance. The interpretation of the results proved to be difficult as some of the results were inconsistent. The spiders did, for instance, respond positively to the exclusion of megaherbivores, but remained unaffected by the exclusion of all herbivores. Many indirect effects of herbivores are, however, only observable at larger scales and it is important to remember that certain patterns might only be explained by spatial differences at the patch scale (Pringle 2008). The results on total abundance revealed that the partial and full enclosure were statistically inseparable, yet both of the experimental treatments differed from the control. This implies that elephants and/or giraffes can have stronger influences on the invertebrate community than medium-sized herbivores.

Giraffes have never been observed at the Nkuhlu enclosures (personal observation; Scogings 2008), and elephants are probably more important than giraffes in affecting invertebrate numbers. Many studies give account of the relative importance of elephants in maintaining open grasslands, and indirect effects (either positive or negative) will likely depend on elephant densities (Pringle 2008).

The mammalian activities at Nkuhlu were also influencing the beetle and orthopteran richness. The beetles and orthopterans were generally more abundant and taxon rich in the partial and full enclosure, where the plant biomass was greater, and even more so in the riparian zone. Perhaps mammalian ungulates compete with orthopterans and beetles for food resources, and affect them negatively by reducing the plant biomass? The results on total abundance also reflect this pattern, probably because most insects are phytophagous (Lawton et al. 1981).

The plant community at Nkuhlu is most likely adapted to intermediate grazing and browsing, and in communities adapted to moderate grazing both very high and very low grazing pressures can be regarded as disturbances (Milchunas et al. 1988). The 'intermediate disturbance hypothesis' states that intermediate disturbances promote biodiversity, and phytophagous invertebrates have been shown to react accordingly as intermediate grazing pressures enhance plant biodiversity (Murdoch et al. 1972, Siemann et al. 1998). This leaves us with the questions: are there too many mammalian herbivores in the KNP, and are they reducing the plant species diversity or just the plant biomass (or both)? Both factors can explain why herbivores at Nkuhlu sometimes reduce the invertebrate richness, since previous studies have shown that a decrease in resource quantity can reduce the invertebrate richness (Dennis et al. 1997, Strand et al. 1999, Suominen et al. 1999).

It is possible that more indirect effects on invertebrates would have been discovered if I had identified them to higher taxonomic resolutions. Furthermore, I can not rule out marked impacts on taxa that are poorly sampled by the trapping methods. The richness can easily

be overestimated as several taxonomic groups, e.g. Araneae and Orthoptera, have many nymph (immature) stages. However, this project did not aim at investigating any particular species. Instead, the main objective was to identify indirect effects, and to put them into a context. Beforehand, I had assumed that the identification at the family level and the trapping period would be sufficient. Indirect effects on invertebrates are, however, likely to be more conspicuous in late summer, as herbivores concentrate in areas with remaining vegetation after extended periods of no rain. Additionally, large taxonomic groups (e.g. orders) are more likely to include many functional groups with different food and habitat preferences.

The sweep nets caught mainly invertebrates associated with the aboveground vegetation (herbaceous layer), and the pitfall traps caught mainly invertebrates living an active existence on the savanna floor. The sampling procedures were, however, only effective in collecting a fraction of the invertebrate orders, families and genera. To obtain a mean within 25 % of the true value, Southwood (1978) estimated that 25 sweeps would be required for the herbaceous layer during sweep-net sampling. Nevertheless, the two trapping procedures belong to the most reliable and practiced methods for sampling epigaeic invertebrates (Samways et al. 1996). There were also some problems with pseudoreplication, since the experiments were restricted to the sites at Nkuhlu. Hence, it is difficult to draw any conclusions for savanna biomes in general from the results. However, the exclosures were very large (50 ha) and the sampling was never restricted to homogenous areas in close proximity of each other, and spillover effects were easily avoided without it compromising the random positioning of samples. Otherwise, edge effects can be problematic. Edge effects of grasshoppers (order: Orthoptera) have, for instance, been found to extend beyond 30 meters (Samways et al. 1991).



Figure 21. Elegant Grasshopper (Photo: Micael Jonsson).

Based on the results, it seems possible that mammalian herbivores have effects on invertebrate communities, but that these effects are site specific and vary across invertebrate taxa. Thus, it is important to realize that the initially asked questions are intertwined, and not independent of each other. The exclosures at Nkuhlu were erected only five years ago. Hence, we might still be observing the effects of herbivory rather than the effects of the river gradient, since time will favour many woody plants (K-selected species). Invertebrates will react differently to herbivory since their preferences in food, microclimate and habitat vary. Activity, breeding and hibernation times might also vary

among invertebrates, and some invertebrates might only emerge during specific seasons, or in the evening instead of early in the morning. Two recommendations for the future would therefore be to narrow down the targeted functional groups, and to collect invertebrates at different times. To begin with, one could for instance concentrate on the phytophagous insects, and collect them in early, mid and late summer. Large scale and long term experiments are, however, required for us to fully understand biodiversity patterns in African savannas.

The results from Nkuhlu provide some insight into the complexity of indirect effects and their potential consequences for management. The results showed that large and medium-sized herbivores can have large indirect effects on the invertebrate richness and abundance, in both arid and productive areas. In the areas that were affected by herbivory, grazing and browsing depressed the invertebrate richness and abundance (see Orthoptera and Coleoptera). One explanation would be that herbivore populations are too large, since the plants are likely to be adapted intermediate grazing and browsing pressures. Another explanation would be that the herbivores congregate in favourable environments, and depress the invertebrate richness and abundance locally but not on a larger scale. Further, there is the matter of whether conditions are natural, or a product of earlier management strategies. Interestingly, elephants have disproportionate effects on the total invertebrate abundance at Nkuhlu, and park authorities of the KNP will have to account for those effects as they start culling elephants.

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Appendix 1. Sweep nets. Taxonomic groups in the experimental treatments (C; control, PE; partial enclosure, FE; full enclosure) and vegetation zones (CR; crest, FS; foot slope, RZ; riparian zone). The presence of a taxonomic group is denoted by x.

Sweep nets	CR			FS			RZ		
	C	PE	FE	C	PE	FE	C	PE	FE
ARACHNIDA	x	x	x	x	x	x	x	x	x
ACARI	x	x	x				x	x	
ARANEAE	x	x	x	x	x	x	x	x	x
Araneidae	x	x	x		x	x		x	x
Corinnidae		x							x
Dictynidae	x		x	x	x	x			
Gnaphosidae								x	
Miturgidae		x		x	x		x	x	x
Oxyopidae	x	x	x	x	x	x	x		x
Philodromidae					x		x		
Pisauridae		x					x		
Salticidae	x	x	x	x	x	x	x	x	x
Sparassidae		x		x	x	x		x	x
Theridiidae	x			x	x				
Thomisidae	x	x	x	x	x	x	x	x	x
<i>Afropisaura</i>		x					x		
<i>Argiope</i>	x		x						
<i>Argyrodes</i>	x								
<i>Asemesthes</i>								x	
<i>Cheiracanthium</i>		x		x	x		x	x	
<i>Cheiramiona</i>					x				x
<i>Corinomma</i>									x
<i>Dictyna</i>	x		x	x	x	x			
<i>Euryopsis</i>				x					
<i>Evarcha</i>	x	x	x	x	x	x	x	x	x
<i>Heliophanus</i>		x			x		x		
<i>Hypsosinga</i>								x	
<i>Latrodectus</i>				x	x				
<i>Monaeses</i>								x	x
<i>Nemoscolus</i>	x	x		x	x				
<i>Neoscona</i>		x		x	x	x	x	x	
<i>Olios</i>		x		x	x	x		x	x
<i>Oxyopes</i>	x	x	x	x	x	x	x	x	x
<i>Pararaneus</i>				x		x			
<i>Peucetia</i>			x						
<i>Runcinia</i>	x	x		x	x		x	x	
<i>Singa</i>				x					x
<i>Suemus</i>					x				
<i>Synema</i>							x		
<i>Theridion</i>				x	x				
<i>Thomisops</i>	x			x				x	
<i>Thomisus</i>			x			x		x	
<i>Thyene</i>								x	
<i>Tibellus</i>							x		
<i>Argiope lobata</i>	x		x						
<i>Cheiramiona paradisus</i>					x				x

<i>Evarcha dotata</i>				x	x	x		x	x
<i>Latrodectus geometricus</i>				x	x				
<i>Monaeses austrinus</i>									x
<i>Nemoscolus cotti</i>	x	x		x	x				
Sweep nets		CR			FS			RZ	
	C	PE	FE	C	PE	FE	C	PE	FE
<i>Nemoscolus tubicola</i>	x	x		x					
<i>Neoscona blondeli</i>							x		
<i>Neoscona subfusca</i>		x		x	x	x		x	
<i>Oxyopes jacksoni</i>		x	x						X
<i>Runcinia affinis</i>				x					
<i>Runcinia flavida</i>	x	x			x			x	
<i>Singa albodorsata</i>				x					x
<i>Synema imitator</i>							x		
<i>Thomisops pupa</i>				x				x	
<i>Thomisus blandus</i>						x			
<i>Thomisus granulatus</i>			x			x			
CHILOPODA			x						
DIPLOPODA	x		x			x	x		
GASTROPODA	x			x					
INSECTA	x	x	x	x	x	x	x	x	x
COLEOPTERA	x	x	x	x	x	x	x	x	x
Chrysomelidae				x	x				x
Coccinellidae		x							
Curculionidae	x	x	x	x		x	x	x	x
Melyridae			x						
Mordellidae						x			
Phalacoidae						x			
Tenebrionidae								x	
COLLEMBOLA	x		x	x	x		x		
DIPTERA		x	x	x	x	x	x	x	x
HETEROPTERA	x	x	x		x	x		x	
HOMOPTERA		x	x	x	x	x	x	x	x
HYMENOPTERA	x	x	x	x	x	x	x	x	x
ISOPTERA									x
MANTODEA	x	x				x		x	x
ORTHOPTERA	x	x	x	x	x	x	x	x	x
Acrididae	x	x	x	x	x	x	x	x	x
Cicadellidae								x	
Eumastacidae					x	x		x	x
Gryllidae	x		x		x				x
Tettigonidae	x		x			x		x	x
<i>Acrotylus</i>			x		x				
<i>Cannula</i>		x							
<i>Catantops</i>									x
<i>Conocephalus</i>			x						
<i>Melidia</i>						x		x	
<i>Oedaleus</i>	x								
<i>Platypternodes</i>						x			
<i>Rhaphotittha</i>		x	x		x	x		x	x
<i>Acrotylus angulatus</i>					x				
<i>Catantops melanostictus</i>									x

<i>Oedaleus plenus</i>	x								
<i>Rhaphotittha levis</i>		x			x	x			x
PHASMATODEA			x	x		x	x		x
PSEUDOSCORPIONIDA							x		x
PSOCOPTERA							x		
THYSANOPTERA			x						

Appendix 2. Pitfall traps. Taxonomic groups in the experimental treatments (C; control, PE; partial enclosure, FE; full enclosure) and vegetation zones (CR; crest, FS; foot slope, RZ; riparian zone). The presence of a taxonomic group is denoted by x.

Pitfall traps	CR			FS			RZ		
	C	PE	FE	C	PE	FE	C	PE	FE
ARACHNIDA	x	x	x	x	x	x	x	x	x
ACARI		x		x	x	x	x	x	x
ARANEAE	x	x	x	x	x	x	x	x	x
CHILOPODA	x			x			x		
CRUSTACEA	x			x	x		x		
DIPLOPODA				x	x	x			
INSECTA	x	x	x	x	x	x	x	x	x
ARCHAEOGNATHA					x	x			
BLATTODEA		x				x		x	x
COLEOPTERA	x		x	x	x	x	x	x	x
COLLEMBOLA	x	x	x	x	x	x	x	x	x
DIPTERA	x	x	x	x	x	x	x	x	x
HETEROPTERA				x	x	x			
HOMOPTERA			x	x	x		x	x	x
HYMENOPTERA	x	x	x	x	x	x	x	x	x
Formicidae	x	x	x	x	x	x	x	x	x
<i>Camponotus</i>								x	
<i>Crematogaster</i>				x					
<i>Dorylus</i>				x					x
<i>Lepisiota</i>								x	
<i>Meranoplus</i>	x								
<i>Monomorium</i>	x	x	x	x	x	x	x	x	x
<i>Myrmicaria</i>	x			x		x	x		
<i>Ocymyrmex</i>	x	x	x	x			x	x	x
<i>Odontomachus</i>							x		x
<i>Pachycondyla</i>				x		x			x
<i>Pheidole</i>	x	x	x		x		x	x	x
<i>Polyrhachis</i>	x								
<i>Tetramorium</i>	x	x					x	x	x
ISOPTERA	x	x		x	x		x		x
ORTHOPTERA	x	x	x	x		x	x	x	x
PSOCOPTERA						x			
THYSANURA									x