



Universiteit
Leiden

The Netherlands

Fire and grazers in the West African savanna

Klop, L.F.

Citation

Klop, L. F. (2009, September 3). *Fire and grazers in the West African savanna*. Retrieved from <https://hdl.handle.net/1887/13947>

Version: Not Applicable (or Unknown)

License: [Licence agreement concerning inclusion of doctoral thesis in the Institutional Repository of the University of Leiden](#)

Downloaded from: <https://hdl.handle.net/1887/13947>

Note: To cite this publication please use the final published version (if applicable).

Chapter 6

**Savanna fires govern community structure of ungulates
in Bénoué National Park, Cameroon**

Erik Klop and Janneke van Goethem

Published in:

Journal of Tropical Ecology 24: 39–47 (2008)

ABSTRACT

We studied the effects of savanna fires on the structure of local ungulate communities in a West African woodland savanna. The distribution of 11 ungulate species over 9–15 burned sites (the number of which increased as burning activity continued during the dry season) and 7–13 unburned sites was compared with a variety of null models or randomized ‘virtual communities’. Five different parameters of community structure were examined: body mass distribution, co-occurrence patterns, species richness, species density and guild dominance. Overall, ungulate species were not randomly distributed over burned and unburned sites. The regular spacing of body masses in the set of species recorded on burned and unburned sites indicated competition, since species similar in body mass are more likely to compete than species of different size. However, co-occurrence patterns on burned sites were random, indicating absence of competition at fine spatial scales due to differential habitat use within the burned landscape. Although the attractiveness of the regrowth on burned sites resulted in higher numbers of ungulates compared with unburned sites, species richness was not different. Grazers were the dominant guild on burned sites, but there were no differences in species richness or species density between grazers and browsers on unburned sites.

Key Words: community ecology, diversity, fire, savanna, species richness, ungulates

6.1 INTRODUCTION

African savannas are well-known for their high species richness of ungulates. Nearly a hundred species of ungulate occur in Africa (Kingdon 1997), and in some areas such as the Serengeti–Mara ecosystem more than 30 of these species coexist (Sinclair & Arcese 1995, Sinclair & Norton-Griffiths 1979). Because of the high species richness of ungulates, the African savannas provide an unparalleled opportunity for studying mechanisms of coexistence (Prins & Olff 1998, Olff *et al.* 2002).

Ungulate assemblages are widely believed to be structured by resource competition and facilitation (Arsenault & Owen-Smith 2002). However, besides biotic interactions, external factors such as rainfall and fire are also considered to be important determinants in shaping assemblages of African ungulates (East 1984, de Bie 1991). Fire is used as a management tool in most African savannas, and plays a significant role in the structure and functioning of these ecosystems (Walker 1981). The significance of fire to grazing ungulates was strongly acknowledged by de Bie (1991), who argued that the ungulate fauna of the West African savanna as a whole should be characterized as a ‘fire climax’. However, it is largely unknown how fires affect herbivore assemblages on a local scale. Fires may alter the distribution of herbivore species because of a change in resource availability (Moe *et al.* 1990, Archibald & Bond 2004). In addition, patterns of resource selection by different ungulates may be governed largely by spatial variation in the quality and structure of the burned grass sward (Klop *et al.* 2007). Finally, species may show differential preference for this post-fire regrowth because of differences in diet (Gureja & Owen-Smith 2002, Tomor & Owen-Smith 2002) or body mass (Wilsey 1996). As a result, fires may govern local patterns of community structure of grazing ungulates.

Non-random patterns of community structure are generally interpreted as the result of ‘assembly rules’ (Diamond 1975, Weiher & Keddy 1999; but see Connor & Simberloff 1979). These assembly rules can be viewed as generalized restrictions to coexistence (Wilson & Whittaker 1995), and represent constraints on how communities are selected as subsets of a larger species pool. Since Diamond’s seminal paper on the assembly of bird communities in the Bismarck Archipelago (Diamond 1975), a large number of studies have tried to demonstrate the existence of such assembly rules. Most of these studies attempted to find patterns in community structure indicating competition, such as reduced body mass overlap (Bowers & Brown 1982, Prins & Olff

1998), guild proportionality (Wilson 1989), and reduced coexistence among potential competitors (Gilpin & Diamond 1982, 1984). However, assembly rules may also be viewed as the way in which communities are shaped by external processes, including disturbances such as fire (Fox 1982, Ratchford *et al.* 2005) or invasion by nonnative species (Sanders *et al.* 2003).

In this paper we investigate whether savanna fires govern the composition of local ungulate assemblages (i.e. the set of species present on either burned or unburned sites) in the Guinea–Sudan savanna of Bénoué National Park, Cameroon. More specifically, we test the hypothesis that species are randomly distributed over burned and unburned sites. In order to test this hypothesis, we focus on five different parameters of community structure: (1) body mass distribution, (2) co-occurrence patterns, (3) species richness, (4) species density and (5) guild dominance. Thus, our main hypothesis can be split into the following hypotheses: (1) the species composition on burned and unburned sites is not different from randomly drawn sets of species taken from the regional species pool; (2) species co-occurrence patterns are similar on burned and unburned sites; (3) ungulate species richness and species density are similar on burned and unburned sites; (4) burned and unburned sites have similar species richness and species density of grazers and browsers.

6.2 METHODS

Study site

This research was carried out in Bénoué National Park (1800 km²), north Cameroon. Annual rainfall ranges from 1200 to 1500 mm with a dry season from November to April. The vegetation can be classified as Guinea–Sudan savanna dominated by *Isoberlinia doka* woodland savanna and *Terminalia macroptera* open savanna (Stark & Hudson 1985). Main grass genera include *Hyparrhenia*, *Andropogon* and *Loudetia* (Stark & Hudson 1985). About 85% of the park was burned by the park management during the dry season of 2003–2004 (with most fires occurring between November and February), in order to facilitate game viewing by tourists and to stimulate regrowth for herbivores.

Table 1. The seventeen species of ungulate recorded in Bénoué N. P., including the eleven species which were recorded during data collection. Body mass data are taken from Kingdon (1997) and refer to the average weight of male and female.

Common name	Species	Body mass (kg)	Guild	Number of individuals recorded	
				Burned	Unburned
Red-flanked duiker	<i>Cephalophus rufilatus</i> Gray	10.0	Browser	64	4
Oribi	<i>Ourebia ourebi</i> Laurillard	17.0	Grazer	161	1
Common duiker	<i>Sylvicapra grimmia</i> Linnaeus	17.5	Browser	45	0
Bohor reedbuck	<i>Redunca redunca</i> Pallas	47.0	Grazer	17	0
Bushbuck	<i>Tragelaphus scriptus</i> Pallas	48.5	Browser	43	5
Red river hog	<i>Potamochoerus porcus</i> Linnaeus	80.0	Omnivorous	0	0
Warthog	<i>Phacochoerus africanus</i> Gmelin	82.5	Grazer	33	8
Kob	<i>Kobus kob</i> Erxleben	85.8	Grazer	1778	25
Korrigum	<i>Damaliscus lunatus korrigum</i> Burchell	126.5	Grazer	0	0
Hartebeest	<i>Alcelaphus bucelaphus major</i> Pallas	161	Grazer	154	4
Waterbuck	<i>Kobus ellipsiprymnus defassa</i> Ogilby	215	Grazer	24	0
Roan	<i>Hippotragus equinus</i> Desmarest	261.3	Grazer	106	1
Derby's eland	<i>Taurotragus derbianus</i> Gray	539.3	Browser	46	0
Buffalo	<i>Syncerus caffer</i> Sparman	550	Grazer	0	0
Giraffe	<i>Giraffa camelopardalis</i> Linnaeus	1340	Browser	n.a.	n.a.
Hippopotamus	<i>Hippopotamus amphibius</i> Linnaeus	1715	Grazer	0	0
African savanna elephant	<i>Loxodonta africana</i> Blumenbach	4000	Mixed Feeder	0	0

A total of 17 species of ungulate occur in the park (Table 1), ignoring the western subspecies of black rhinoceros (*Diceros bicornis longipes*) which is likely to be extinct (www.iucn.org/en/news/archive/2006/07/7_pr_rhino.htm).

Data collection

Data were collected by driving along road transects throughout the park. Four transects were selected, ranging in length from 24 to 36 km. Data collection started in December 2003 and ended in May 2004, thus covering the entire dry season and the onset of the wet season. All transects were traversed at regular 18-d intervals, each transect being sampled nine times. A part of the dataset used here is the same as used for a resource-selection study (Klop *et al.* 2007), although in this study the data from unburned sites are added to the dataset. The number of burned and unburned sites covered by the transects was dynamic as burning activity continued during the data collection period, and varied from 9 to 15 burned sites and 7 to 13 unburned sites. Around 60% of the area covered by the transects was burned at the outset of the data collection period, increasing to around 85% at the end of the dry season. Burning has been shown to attract both grass-eating ('grazing') and foliage-eating ('browsing') ungulates by stimulating grass regrowth as well as the sprouting of some dicot herbs and trees (Klop *et al.* 2007). Hence, in this study we consider both grazers and browsers, the feeding stratum of which is affected by fire. The giraffe is ignored in this study because its feeding stratum is well above the direct range of influence of both fire and other species of herbivore. For every ungulate encountered, the species, location and habitat (i.e. burned or unburned) were recorded. The observations were grouped into samples, whereby all observations from a given transect on a given date constitute one sample. This results in 9 (periods) \times 4 (transects) = 36 samples. Autocorrelation of the observations along the same transect at different times was tested using a Mantel test (Legendre & Legendre 1998). No significant correlation could be found between ecological distance (Bray–Curtis dissimilarities) and time lag ($Z=-0.08$, $P=0.09$). The data were organized into species-by-sites matrices, where each row represents a species and each column represents a sample. Since all samples contain both burned and unburned sites, the matrices were partitioned into data from burned sites and unburned sites. This effectively doubles the number of samples to a total of 72.

All analyses of co-occurrence patterns and randomness of body mass distribution were carried out using the program EcoSim (<http://homepages.together.net/~gentsmin/ecosim.htm>). All simulation algorithms were run using 5000 iterations. Deviation from randomness was considered significant when the observed index fell in the extreme upper or lower tail (each set at 2.5%) of the range of simulated values.

Randomness of body mass distribution

The analysis of body mass distribution follows Gotelli and Ellison (2002). Firstly, body size data were ranked and log₁₀-transformed to enable the analysis of size ratios. The difference in size between two adjacent species can be viewed as a segment of certain length. The variance in segment length is used as a measure of the variability in body size ratios, since a constancy in size ratios leads to identical segment lengths and hence the variance will be nil (0) (Poole & Rathcke 1979). Thus, if a community shows regularity in body size distribution, the observed variance should be significantly less than expected by chance. Body mass data are taken from Kingdon (1997) and were calculated as the average weight of male and female. In order to test the null hypothesis that the body mass distributions of ungulate assemblages on burned and unburned sites are not different from what could be expected by chance, three different null models were used (Gotelli & Ellison 2002): (1) Uniform – in this null model the logarithms of body masses of all species are arranged as points along a line, with the end points set by the smallest and largest body mass observed in the assemblages on either burned or unburned sites. Constancy of body mass ratio would mean equidistant placement of the body masses along this line (Simberloff & Boecklen 1981, Gotelli & Graves 1996). For each null assemblage, $n - 2$ points (i.e. body masses of 'virtual species') are drawn randomly and uniformly between the end points. The observed variance in segment length is then compared to the mean simulated variance. (2) Equiprobable source pool – in this null model, species are drawn randomly and equiprobably from the total species pool of Bénoué N. P. Once drawn, a species cannot be selected again. In contrast to the uniform model, here the possible body masses of 'virtual species' are constrained to match those of real species in the Bénoué species pool, and the endpoints of the body size distribution are represented by the body mass of the smallest and largest species in the total species pool. (3) Abundance-weighted source pool – here species are also drawn randomly from the Bénoué species list, but the probability of being drawn is proportional to the abundance of that species. We used the population densities in Bénoué N. P. as a measure of abundance. Data on population densities are from Mayaka

(2002), except for red river hog, korrigum, buffalo, hippopotamus and African savanna elephant, for which no accurate recent data on population densities are available. Instead, we simply divided the estimated population sizes in Bénoué N. P. (based on professional judgement by the park management and our own observations) by the total area of the park.

Co-occurrence patterns

Co-occurrence patterns on burned and unburned sites were quantified by the C-score (Stone & Roberts 1990), which is a measure of average pairwise species co-occurrence. The larger the C-score, the less is the average co-occurrence (Gotelli 2000, Gotelli & Ellison 2002). All co-occurrence analyses refer to average co-occurrence patterns at the level of the entire community. To test whether co-occurrence patterns are random across burned and unburned sites, we used a simple randomization test similar to that used by Stone *et al.* (1996, 2000) and Sanders *et al.* (2003). Within the incidence matrix containing the data from burned and unburned sites, we randomly reshuffled the site labels (i.e. burned or unburned). A set of 5000 randomized matrices was generated, for each of which the C-score and its variance were calculated. The observed C-score and variance of the burned and unburned sites were then compared to the set of randomly reshuffled matrices. Co-occurrence patterns within burned and unburned sites were tested by comparing the C-score of the observed data to a suitable null model (Gotelli & Graves 1996), i.e. a matrix in which the occurrence of each species is randomly assigned to a site. We used a simulation algorithm in which both the row and column sums of the original matrix are preserved. Thus, the number of species in each random community is the same as in the original community, and each species occurs at the same frequency as in the original dataset (Connor & Simberloff 1979, Gotelli & Ellison 2002). This algorithm has been shown to behave well (i.e. low frequencies of Type I and Type II errors) when tested against random and nonrandom matrices (Gotelli 2000).

Species richness and density

Species richness of burned and unburned sites was compared using rarefaction (Simberloff 1972). A sample-based approach was used to account for sample heterogeneity in space and time (Colwell *et al.* 2004, Gotelli & Colwell 2001). Sample-based rarefaction permits comparison of different assemblages at comparable levels of sampling effort (Colwell *et al.* 2004). In order to

allow comparison of species richness between burned and unburned sites, the rarefaction curves were rescaled to individuals (Gotelli & Colwell 2001). Likewise, the rarefaction curves were re-scaled to samples to allow comparison of species density. When samples are purely spatial, the measure of species density can be interpreted as the number of species per unit area (Gotelli & Colwell 2001). However, in our study, samples constitute both a spatial and temporal component and species density should therefore be interpreted as the number of species per unit effort. Rarefaction analyses were based on the analytically computed estimator τ (Colwell *et al.* 2004), using the program EstimateS (<http://viceroy.eeb.uconn.edu/EstimateS>).

Guild dominance

The distribution of the species in different guilds over burned and unburned sites was analysed using the same techniques as described in the previous section. In the analyses we have assigned the species into the following guilds: (1) grazers with more than 80% grass in their diet, (2) mixed feeders with 20–80% grass in their diet and (3) browsers with less than 20% grass in their diet (Table 1).

6.3 RESULTS

When using the uniform null model, the body mass distributions on both burned and unburned sites were not significantly different from what would be expected by chance (Table 2). In contrast, both the equiprobable and the abundance-weighted null model result in a body mass distribution that was significantly more regular on both burned ($P < 0.01$) and unburned sites ($P < 0.05$) than in assemblages that are randomly drawn from the Bénoué species pool. The degree of co-occurrence on burned sites was significantly lower than on unburned sites ($P < 0.01$) (Table 3). Within burned sites, the observed *C*-score was not significantly different from random ($P = 0.31$). In contrast, co-occurrence within unburned sites was significantly higher (i.e. a lower *C*-score) than expected by chance ($P < 0.01$).

As shown by the overlapping 95% confidence intervals of the rarefaction curves for species richness (Figure 1a), there was no significant difference in species richness between burned and unburned sites. On the contrary, the species density on unburned sites was significantly lower than on burned sites (Figure 1b).

On burned sites, both species richness and species density of grazers were higher than those of browsers (Figure 2a, b). On unburned sites there was no significant difference in either species richness or species density between grazers and browsers (Figure 2c, d).

Table 2. Randomness of body mass distribution on burned and unburned sites. The first column lists the three different null models applied to both burned and unburned sites.

Null model	Observed index	Simulated index	Variance	P
Burned uniform	0.021	0.027	<0.001	0.397
Unburned uniform	0.020	0.048	0.001	0.138
Burned equiprobable	0.021	0.033	<0.001	0
Unburned equiprobable	0.020	0.042	0.001	0.035
Burned abundance-weighted	0.021	0.033	<0.001	0

Table 3. Co-occurrence analysis of burned versus unburned sites. *n* is the number of samples. The results in the first row show whether the mean co-occurrence index across all sites is larger or smaller than expected by chance. The results in the second row show the results for burned versus unburned sites. The third and fourth rows show whether co-occurrence patterns within burned and unburned sites are distinct from random.

	n	Observed C-score	Mean simulated C-score	Variance simulated C-score	P
All sites	72	55.2	55.2	0.57	0.551
Burned vs. unburned	72	21.2	13.8	0.37	0
Within burned	36	38.3	38.7	0.39	0.309
Within unburned	36	4.0	4.4	0.04	0.008

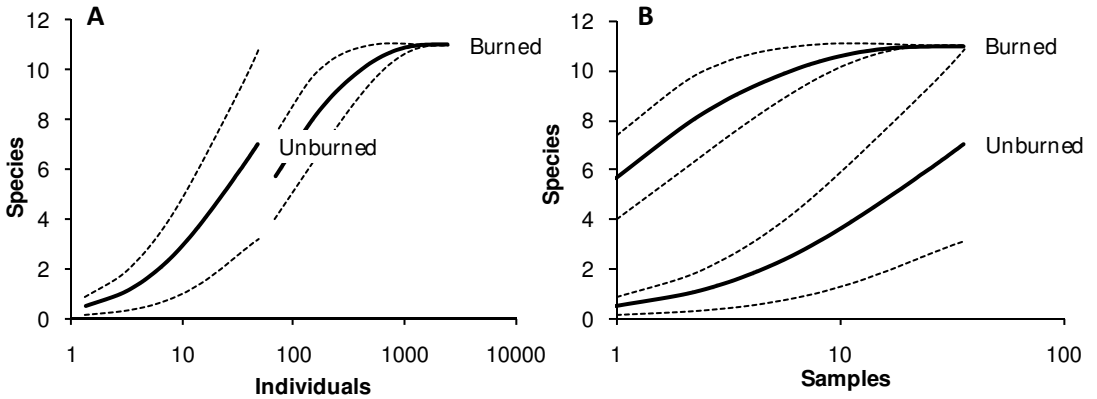


Fig. 1. Species richness (a) and species density (b) of ungulates on burned versus unburned sites. The rarefaction curves are shown by the bold lines, whereas their 95% confidence intervals are shown by the dashed lines.

6.4 DISCUSSION

Body mass distribution

According to the equiprobable and abundance-weighted null models, the body mass distributions of the total set of species recorded on burned and unburned sites were significantly more regular than those of assemblages that were randomly drawn from the Bénoué species pool. That is, each species in the assemblage was, on average, a constant proportion larger than the next smaller one (Prins & Olff 1998). Non-random patterns in body mass distribution may be the result of allometric patterns of resource use, biotic interactions and geographical and evolutionary constraints on community organization (Allen *et al.* 2006). Two processes may account for the observed regularity in body mass distributions. First, from classical competition theory it follows that the body masses of sympatric species need to be separated by a constant factor in order to permit coexistence at the same trophic level (Hutchinson 1959). Based on this theory, Prins & Olff (1998) argued that a regular body mass distribution is expected in herbivore assemblages because herbivores of similar size are likely to compete for the same resources. Although the relation between body mass distribution and competition is controversial (Horn & May 1977), at the scale of local assemblages competition is

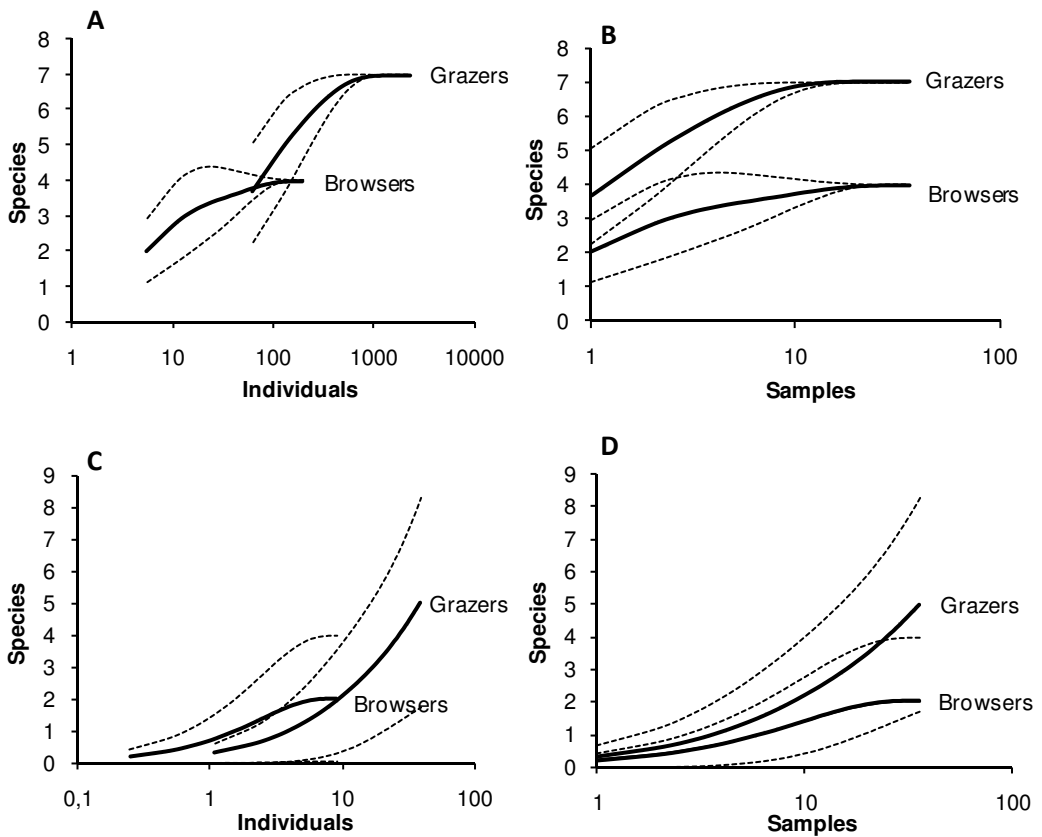


Fig. 2. Species richness (a, c) and species density (b, d) of grazers versus browsers on burned (a, b) and unburned (c, d) sites. The rarefaction curves are shown by the bold lines, whereas their 95% confidence intervals are shown by the dashed lines.

the most likely process explaining patterns in body mass distributions (Allen *et al.* 2006). A second explanation for the regularity in body mass distributions refers to the spatial scaling of resource use by species of different size (Ritchie & Olff 1999). Different species perceive the environment at a scale of resolution which is determined by their respective body size (Ritchie & Olff 1999, Allen *et al.* 2006). Thus, when species of different size select different sites based on the spatial structure of the vegetation and habitat, this will be reflected in the body mass distribution in a community (Holling 1992, Ritchie & Olff 1999). The use of burned areas may also be affected by body mass because of differential preference for post-fire regrowth (Wilsey 1996) or differences in mobility between species of different size. However, no effect of body mass on the use of burned areas by grazing ungulates was found in other studies (Tomor & Owen-Smith 2002, Klop *et al.* 2007).

In contrast to the equiprobable and abundance-weighted null models, the uniform model did not find any significant differences in the body mass distributions of real and randomized communities. The use of null models has often been criticized for inconsistent results when using different algorithms, or when different amounts of 'biological realism' are incorporated in the model (Gotelli & Graves 1996). The different outcome of the uniform model is likely to be the result of the fact that in this model, the body masses of virtual species are generated randomly within the boundaries that are set by the smallest and largest species observed in the community, rather than drawing body masses from a larger species pool.

Co-occurrence patterns

Average co-occurrence on burned sites was significantly lower than on unburned sites. That is, within burned sites co-occurrence patterns appeared to be random, whereas unburned sites showed aggregated co-occurrence patterns. Competition for resources may lead to lower than expected average co-occurrence (Diamond 1975), and the random co-occurrence patterns on burned sites suggest that competitive or facilitative interactions are absent or low (Gotelli & Graves 1996, but see Hastings 1987). However, the effects of competition in herbivore communities may be more subtle than those manifested in presence-absence data (Redfern *et al.* 2006), and even strong competition may remain undetected by analysing species co-occurrence data (Hastings 1987). Many studies have tried to demonstrate competition in ungulate communities (Gordon & Illius 1989, Hobbs *et al.* 1996, Murray & Illius 2000) and its importance in governing community structure is widely accepted (Arsenault & Owen-Smith 2002). The fact that co-occurrence patterns are random whereas the overall body mass distribution is not, suggests that differences in the spatial distribution of ungulate species (as a result of e.g. differential habitat preferences or water dependency) preclude competition. For example, highly water-dependent species such as kob, reedbuck and waterbuck are not likely to compete with species found farther away from water sources such as hartebeest and roan. Thus although the total set of species using burned sites may be structured by biotic interactions, at finer spatial scales competition may be absent or low because of the ecological separation of different ungulate species.

In contrast to the assemblages on burned sites, the assemblages on unburned sites show aggregated co-occurrence patterns, i.e. on average species co-occur more often than expected by chance. This may be because of facilitative interactions, where the grazing of one species enhances the accessibility of high-quality grass leaves to

other species by removing the lower-quality components such as stems and dead leaves from the grass sward. However, the evidence for facilitation in ungulate communities due to increased resource access through removal of obstructing grass parts during the dormant season is weak (Arsenault & Owen-Smith 2002). Although grazing facilitation in Bénoué N. P. is an important mechanism in ungulate communities during the wet season (Verweij *et al.* 2006), we found no indication of grazing facilitation on unburned sites during the dry season when grasses are dormant. Instead, it is more likely that the aggregated co-occurrence patterns on unburned sites resulted from the use of patches of tall and dense grass by several species as escape cover to avoid predation (Moe *et al.* 1990).

Species richness, species density and guild dominance

It is no surprise that species density is lower on unburned sites than on burned sites, as the number of observations from unburned sites was extremely low. The high numbers of grazing ungulates on post-fire regrowth compared to unburned areas have been described numerous times (Moe *et al.* 1990, Moe & Wegge 1997, Wilsey 1996, Gureja & Owen-Smith 2002, Tomor & Owen-Smith 2002, Archibald & Bond 2004, Archibald *et al.* 2004,). However, when the number of species is standardized by the number of individuals there is no significant difference in species richness. The analyses of guild dominance showed that grazers reached higher species richness and species density than browsers on burned sites. Although the higher species richness of grazers on burned sites may reflect the abundance of grass regrowth, it may also be an artefact of the fact that the overall species list of Bénoué N. P. contains more grazers than browsers (Table 1). In addition, the higher species density of grazers may be caused to a large extent by kob, which is by far the most abundant species of ungulate in the park.

Data considerations

The data show considerable differences in animal numbers that were recorded on burned versus unburned sites. The low number of observations on unburned sites may result from reduced visibility caused by the high grass, leading to 'false absences' (MacKenzie *et al.* 2004). However, the distribution of observations across burned and unburned sites along the transects is consistent with the data from hundreds of hours of observations from elevated observation platforms, with good visibility even in high grass (Klop & van Goethem unpubl. data). Nevertheless, imperfect detection in high

grass may have affected the observations of, in particular, some of the smaller species such as oribi and the two species of duiker.

The severely unbalanced datasets for burned and unburned sites may raise the question whether valid comparisons can still be made. However, the analysis techniques used in this study are robust to variation in the numbers of animals recorded. First, the analyses of species richness and guild dominance are not affected by different sample sizes, since the rarefaction curves are by definition re-scaled to the number of individuals. Second, the analyses of body mass distributions and co-occurrence patterns are based on presence-absence data and hence, differences in the number of animals recorded are not taken into account.

6.5 CONCLUSION

Our results show that herbivores are not randomly distributed over burned and unburned sites. Rather, fires lead to non-random patterns in body mass distribution, and differences in co-occurrence patterns, species density and guild dominance between burned and unburned sites. We suggest that the response of herbivore communities to fire is likely to be the compound effect of various factors, including changes in habitat structure, resource selection patterns, predator avoidance and biotic interactions such as competition. In addition, the effects of fire on ungulate community structure may depend on time of burning in the season, the extent of burning and the availability of other high-quality grass swards on, for example, grazing lawns and floodplains. Patterns of community assembly of ungulates in Bénoué N. P. may be very different during the wet season, when many species of grazers have left the post-fire regrowth for the grazing lawns of hippopotamus (Verweij *et al.* 2006).

Fires may also affect coexistence on larger spatial and temporal scales. For example, at the scale of Bénoué N. P. or even that of West Africa, the distribution of ungulate species is likely to be affected by the regular occurrence of fires. For example, short-grass grazers such as kob and oribi may not be able to persist in the moist Guinea savanna without being 'facilitated' by fire. However, empirical data on this scale are scarce and the long-term effects of fires on species coexistence need further study. Nonetheless, our results show that during the dry season and on a local scale, savanna fires are a major factor governing ungulate community structure.

REFERENCES

- Allen, C.R., Garmestani, A.S., Havlicek, T.D., Marquet, P.A., Peterson, G.D., Restrepo, C., Stow, C.A. and Weeks, B.E. (2006). Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters* 9: 630-643.
- Archibald, S. and Bond, W.J. (2004). Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire* 13: 377-385.
- Archibald, S., Bond, W.J., Stock, W.D. and Fairbanks, D.H.K. (2004). Shaping the landscape: fire-grazer interactions in an African savanna. *Ecological Applications* 15: 96-109.
- Arsenault, R. and Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97: 313-318.
- Bowers, M.A. and Brown, J.H. (1982). Body size and co-existence in desert rodents: chance or community structure? *Ecology* 63: 391-400.
- Colwell, R.K., Mao, C.X. and Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85: 2717-2727.
- Connor, E.H. and Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.
- De Bie, S. (1991). *Wildlife resources of the West African Savanna*. PhD thesis, Wageningen Agricultural University.
- Diamond, J. (1975). Assembly of species communities. Pp. 342-444 in Cody, M.L. and Diamond, J.M. (eds.) *Ecology and evolution of communities*. Harvard University Press, Cambridge.
- East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology* 22: 245-270.
- Fox, B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63: 1332-1341.
- Gilpin, M.E. and Diamond, J.M. (1982). Factors contributing to non-randomness in species co-occurrences on islands. *Oecologia* 52: 75-84.
- Gilpin, M.E. and Diamond, J.M. (1984). Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? Pp. 297-315 in Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B. (eds.) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton.

- Gordon, I.J. and Illius, A.W. (1989). Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 79: 383-389.
- Gotelli, N.J. (2000). Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621.
- Gotelli, N.J. and Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379- 391.
- Gotelli, N.J. and Ellison, A.M. (2002). Assembly rules for New England ant assemblages. *Oikos* 99: 591-599.
- Gotelli, N.J. and Graves, G.R. (1996). *Null models in ecology*. Smithsonian Institution Press, Washington DC.
- Gureja, N. and Owen-Smith, N. (2002). Comparative use of burned grassland by rare antelope species in a lowveld ranch, South Africa. *South African Journal of Wildlife Research* 32: 31-38.
- Hastings, A. (1987). Can competition be detected using species co-occurrence data? *Ecology* 68: 117-123.
- Hobbs, N.T., Baker, D.L., Bear, G.D. and Bowden, D.C. (1996). Ungulate grazing in sagebrush grassland: mechanisms of resource competition. *Ecological Applications* 6: 200-217.
- Holling, C.S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62: 447-502.
- Horn, H.S. and May, R.M. (1977). Limits to similarity among coexisting competitors. *Nature* 270: 660-661.
- Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93: 145-159.
- Kingdon, J. (1997). *The Kingdon field guide to African mammals*. Academic Press, San Diego.
- Klop, E., Van Goethem, J. and De longh, H .H. (2007). Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research* 34: 77-83.
- Legendre, P. and Legendre, L. (1998). *Numerical ecology, second edn*. Elsevier, Amsterdam.
- MacKenzie, D.I., Bailey, L.L. and Nichols, J.D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73: 546-555.
- Mayaka, T.B. (2002). *Value Wildlife! An ecological and economic assessment of wildlife use in northern Cameroon*. PhD thesis, Leiden University.

- Moe, S.R. and Wegge, P. (1997). The effects of cutting and burning of grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. *Journal of Tropical Ecology* 13: 279-292.
- Moe, S.R., Wegge, P. and Kapela, E.B. (1990). The influence of man-made fires on large wild herbivores in Lake Burungi in northern Tanzania. *African Journal of Ecology* 28: 35-43.
- Murray, M.G. and Illius, A.W. (2000). Vegetation modification and resource competition in grazing ungulates. *Oikos* 89: 501-508.
- Olf, H., Ritchie, M.E. and Prins, H.H.T. (2002). Global environmental controls of diversity in large herbivores. *Nature* 415: 901-904.
- Poole, R.W. and Rathcke, B.J. (1979). Regularity, randomness, and aggregation in flowering phenologies. *Science* 203: 470-471.
- Prins, H.H.T. and Olf, H. (1998). Species-richness of African grazer assemblages: towards a functional explanation. Pp. 449-490 in Newbery, D.M., Prins, H.H.T. and Brown, N. (eds.) *Dynamics of tropical communities*. Blackwell Science, Oxford.
- Ratchford, J.S., Wittman, S.E., Jules, E.S., Ellison, A.M., Gotelli, N.J. and Sanders, N.J. (2005). The effects of fire, local environment and time on ant assemblages in fens and forests. *Diversity and Distributions* 11: 487-497.
- Redfern, J.V., Ryan, S.J. and Getz, W.M. (2006). Defining herbivore assemblages in the Kruger National Park: a correlative coherence approach. *Oecologia* 146: 632-640.
- Ritchie, M.E. and Olf, H. (1999). Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400: 557-560.
- Sanders, N.J., Gotelli, N.J., Heller, N.E. and Gordon, D.M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences, USA* 100: 2474-2477.
- Simberloff, D. (1972). Properties of the rarefaction diversity measurement. *American Naturalist* 106: 414-418.
- Simberloff, D. and Boecklen, W. (1981). Santa Rosalia reconsidered: size ratios and competition. *Evolution* 35: 1206-1228.
- Sinclair, A.R.E. and Arcese, P. (eds.) (1995). *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago.
- Sinclair, A.R.E. and Norton-Griffiths, M. (eds.) (1979). *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago.
- Stark, M.A. and Hudson, R.J. (1985). Plant communities in Bénoué National Park, Cameroon: a cluster association analysis. *African Journal of Ecology* 23: 21-27.

- Stone, L. and Roberts, A. (1990). The checkerboard score and species distributions. *Oecologia* 85: 74-79.
- Stone, L., Dayan, T. and Simberloff, D. (1996). Community-wide assembly patterns unmasked: the importance of species' differing geographic ranges. *American Naturalist* 148: 997-1015.
- Stone, L., Dayan, T. and Simberloff, D. (2000). On desert rodents, favored states, and unresolved issues: scaling up and down regional assemblages and local communities. *American Naturalist* 156: 322-328.
- Tomor, B.M. and Owen-Smith, N. (2002). Comparative use of grass regrowth following burns by four ungulate species in Nylsvlei Nature Reserve, South Africa. *African Journal of Ecology* 40: 201-204.
- Verweij, R.J.T., Verrelst, J., Loth, P.E., Heitkönig, I.M.A. and Brunsting, A.M.H. (2006). Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos* 114: 108-116.
- Walker, B.H. (1981). Is succession a viable concept in African savanna ecosystems? Pp. 431-447 in West, D.C., Shugart, H.H. and Botkin, D.B. (eds.) *Forest succession*. Springer-Verlag, Berlin.
- Weiher, E. and Keddy, P. (eds.) (1999). *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge.
- Wilsey, B.J. (1996). Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology* 34: 32-38.
- Wilson, J.B. (1989). A null model of guild proportionality, applied to stratification of a New Zealand temperate rain forest. *Oecologia* 80: 263-267.
- Wilson, J.B. and Whittaker, R.J. (1995). Assembly rules demonstrated in a saltmarsh community. *Journal of Ecology* 83: 801-807.

