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Fire and grazers in the West African savanna

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Chapter 7

Diversity and species composition of West African ungulate assemblages: effects of fire, climate and soil

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ABSTRACT

Aim

Anthropogenic fires are a major component of the ecology of rangelands throughout the world. To assess the effects of these fires on the diversity patterns of herbivores, we related gradients in fire occurrence, climate and soil fertility to patterns in alpha and beta diversity of African ungulates.

Location

West Africa.

Methods

We used a survey-based approach for ungulates in 37 protected areas in desert, savanna and rain forest habitats throughout West Africa, combined with satellite images of fire occurrence and digital maps of actual evapotranspiration and soil fertility. Alpha diversity was related to the environmental variables using conventional and spatial regression models. We investigated beta diversity using partial Mantel tests and ordination techniques, and by partitioning the variance in assemblage composition into environmental and spatial components.

Results

The species richness of grazers showed a quadratic relationship with actual evapotranspiration, whereas that of browsers and frugivores showed a linear relationship. However, in the multiple regression models fire occurrence was the only variable that significantly correlated with the species richness of grazers. Soil fertility was weakly related to overall beta diversity and the species richness of browsers, but was non-significant in the multiple regression models. Fire occurrence was the most important variable explaining species composition of the overall species set and of grazers, whereas the assemblage composition of browsers and frugivores was explained mostly by actual evapotranspiration.

Main conclusions

In contrast to previous studies, our analyses show that moisture and nutrients alone fail to adequately predict the diversity patterns of grazing ungulates. Rather, the species richness and assemblage composition of grazers are largely governed by anthropogenic fires that modify the quality and structure of the grass sward. Diversity patterns of browsers and frugivores are markedly different from grazers and depend mainly on the availability of moisture, which is positively correlated with the availability of foliage and fruits. Our study highlights the importance of incorporating major human-induced disturbances or habitat alterations into analyses of diversity patterns.

Keywords

Actual evapotranspiration, anthropogenic effects, community composition, diversity, fire, soil fertility, spatial effects, species richness, ungulates, variance partitioning.

7.1 INTRODUCTION

The factors that drive global or regional patterns in species richness continue to be a main focus of ecological research (Rosenzweig 1995, Hawkins *et al.* 2003). Diversity gradients of terrestrial vertebrates have been explained by a plethora of hypotheses, mostly focusing on climate-based parameters such as water, energy or composite measures such as actual evapotranspiration (Hawkins *et al.* 2003).

In a recent paper, Olff *et al.* (2002) showed that global diversity patterns of mammalian herbivores are largely governed by the moisture available to plants and soil fertility. Since moisture availability determines plant production, and hence forage availability, there is a rainfall threshold below which productivity will be insufficient to support populations of large herbivores (Olff *et al.* 2002). However, forage quality declines with increasing productivity (Breman & De Wit 1983) due to a decline in the ratio of leaf tissue nitrogen to the poorly digestible carbohydrates cellulose and lignin. Because ruminating herbivores need a minimum of 7% crude protein in their food to support rumen fermentation (Breman & De Wit 1983, Prins, 1996), these herbivores face a trade-off between forage quality and quantity. As a result, the highest diversity of herbivores is expected in areas with intermediate moisture and high soil nutrients (Olff *et al.* 2002).

The African savannas support high species richness and biomass of mammalian herbivores (Prins & Olff 1998, Olff *et al.* 2002). Besides environmental factors such as moisture and soil fertility, annual savanna fires are an important determinant of the herbivore community (De Bie 1991). About one-half of the global amount of savanna biomass burning is concentrated in Africa (Andreae 1990), and anthropogenic fires are an important feature of the West African savanna (Fig. 1). Although areas are burned for many reasons, fires are often set with the purpose of creating grass regrowth for herbivores, as savanna fires bring about significant changes in forage quality and quantity. By setting fire to high-biomass grass swards, cattle herders and park managers allow either domestic or wild herbivores to graze on high-quality grass regrowth in areas where the quality of the vegetation would otherwise be below herbivore maintenance levels. Post-fire regrowth has higher nutrient levels, higher leaf:stem ratios and higher digestibility than unburned vegetation (Van de Vijver *et al.* 1999), and it is well known that grazing herbivores are attracted by post-fire regrowth because of the superior forage quality and more favourable sward structure. The response of herbivores to fires depends on the feeding guild, however. Although burning can also attract browsers by

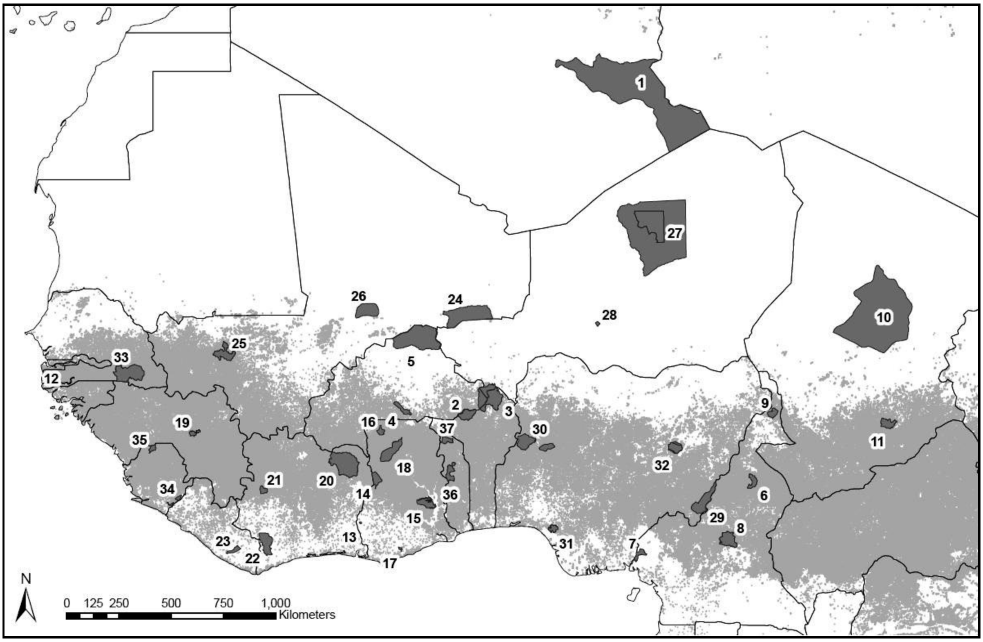

Fig. 1. Fires recorded in the study area in 2006 based on Modis satellite observations (Justice *et al*. 2002). Each fire pixel represents an area of approximately 1 km^2 in which at least one fire was observed. The shaded polygons are the protected areas (WDPA, 2006) covered by this study. 1: Tassili N'Ajjer, 2: Pendjari, 3: W, 4: Kabore Tambi, 5: Sahel, 6: Bénoué, 7: Korup, 8: Mbam Djerem, 9: Waza, 10: Ouadi Rime Ouadi Achim, 11: Zakouma, 12: Kiang West, 13: Bia, 14: Bui, 15: Digya, 16: Gbele, 17: Kakum, 18: Mole, 19: Haut Niger (Mafou & Amana Forests), 20: Comoe, 21: Mont Sangbe, 22: Tai, 23: Sapo, 24: Ansongo Menaka, 25: Boucle du Baoule, 26: Gourma, 27: Air Tenere (incl. Addax Reserve), 28: Gadabedji, 29: Gashaka Gumti, 30: Kainji Lake, 31: Okomu, 32: Yankari, 33: Niokolo Koba, 34: Gola, 35: Outamba Kilimi, 36: Fazao Malfakassa, 37: Keran.

stimulating the sprouting of forbs and trees (Klop *et al*. 2007), fires are of particular importance to grazers by replacing the entire moribund grass sward with regrowth.

The vast extent of savanna burning and the resulting changes in forage quality may affect regional diversity patterns of herbivores, especially if one realizes that forest has been rolled back at a continent-wide scale to the benefit of savannas after millennia of burning (Bond & Keeley 2005). Savanna fires have been shown to affect some parameters of ungulate assemblage structure at a local scale such as co-occurrence patterns and guild dominance (Klop & Van Goethem 2008), but it is unclear whether and how fires affect the broad-scale diversity patterns of ungulates. In addition, it is unknown to what extent guild membership affects diversity patterns in relation to fires or environmental variables such as moisture and nutrient availability. In this paper we attempt to relate patterns in species richness (alpha diversity) and differences in species composition between ungulate assemblages (beta diversity) to gradients in fire occurrence, actual evapotranspiration and soil fertility throughout western Africa. We consider both the entire species set of West African ungulates as well as the two main guilds, i.e. grazers versus browsers/frugivores. Our research questions are thus as follows: (1) to what extent are patterns in species richness and assemblage composition of ungulates related to patterns in fire occurrence, productivity and soil fertility; and (2) does the relation between the environmental variables and herbivore diversity differ among guilds?

7.2 METHODS

Data collection

We compiled a database on the occurrence of all ungulate species (grandorder Ungulata; Duff & Lawson 2004) in a number of protected areas scattered throughout western Africa (Fig. 1). Our study area is bounded by central Algeria in the north and the Chadian–Sudanese border in the east. We selected protected areas in all habitats ranging from the Sahara Desert to rain forest. Areas for which we considered the information on species composition to be incomplete, uncertain or conflicting between sources were excluded from the database. This resulted in a selection of 37 areas in 16 countries, containing a total of 43 ungulate species (see Appendices S1 and S2 in Supporting Information). The main source of information on the distribution of antelopes and buffalo (family Bovidae) were the antelope surveys and their updates published by the IUCN Antelope Specialist Group (East 1990, 1995–2001, Mallon & Kingswood 2001, Chardonnet & Chardonnet 2004). Information on the distribution of elephant, rhinoceros, giraffe, sheep, hippopotamus and pigs was taken from Blanc *et al.* (2007), Emslie & Brooks (1999), Ciofolo (1995), Shackleton (1997) and Oliver (1993), respectively. This information was supplemented by and crosschecked with country-specific information on Nigeria (Happold, 1987), Ghana, Sierra Leone and the Gambia (Grubb *et al.* 1998), data from Haut Niger in Guinea (Ziegler *et al.* 2002), reports on Sahelo-Saharan species (Beudels *et al.* 2005), various unpublished management plans and personal observations in some of the areas. Species that are known to have recently gone extinct in some of the areas were treated as if still extant. Each species was assigned to a guild (grazer, browser, frugivore, intermediate feeder and generalist) based on Gagnon & Chew (2000) and Kingdon (1997) (see Appendix S2), although we have not adopted Gagnon & Chew's (2000) subdivision of grazers into strict and variable grazers.

Fire occurrence in western Africa was calculated from Modis satellite images (Justice *et al.* 2002) showing all fire detections in the years 2003–06. Since no reliable data on fire occurrence are available for earlier or longer time periods, this 4-year period was considered to be representative of the general pattern in fire distribution in West Africa. Each fire detection represents a pixel of approximately 1 km2 in which at least one fire was observed in a given calendar year. The minimum detectable fire size at a detection probability of 50% is around 100 m2 , depending on cloud cover, smoke, habitat, sun position etc. Further details on the Modis fire maps are given by Justice *et al.* (2002). The occurrence of fires in each protected area was assessed by overlaying the fire map with a map showing the boundaries of the selected areas published by the World Database on Protected Areas (WDPA 2006; http://www.unep-wcmc.org/wdpa/). Fire density was then calculated as the mean number of fire pixels per year inside the boundaries of each protected area, divided by the area in km^2.

In addition to fire density, predictor variables included actual evapotranspiration (AET) and soil fertility. Area size was not incorporated as a predictor variable, since the huge size of many protected areas in the thinly populated desert zone compared with the much smaller areas set aside for conservation in the more densely populated savanna and forest zones may lead to false conclusions relating species richness to area size. Data on annual AET were based on Ahn & Tateishi (1994) and were read at a resolution of 0.5° (which equals about 55.6×55.6 km ≈ 3100 km^2 at the equator) from a digital map (www.grid.unep.ch/data/data.php?category=atmosphere). Information on soil fertility was taken from the digital global map of derived soil properties of ISRIC World Soil Information (Batjes 2006; www.isric.org/UK/About+Soils/Soil+data/Geographic+data/Global/WISE5by5minutes.htm). The soil parameters are for the depth layer of 0–20 cm and were read at a grid cell resolution of five by five arc-minutes (equalling about 9.3×9.3 km ≈ 86 km^2 at the equator). The following soil parameters were used: cation exchange capacity (CEC, in $cmol_c$ kg^{-1}) of the fine earth fraction, total organic carbon content (in g kg^{-1}) and total nitrogen (g kg^{-1}). Mean values of AET (mm $year^{-1}$) and the soil parameters for each protected area were calculated by overlaying the soil map by the protected areas map (WDPA 2006). Only those grid cells for which the centre fell inside the protected area boundaries were used for calculating mean values of the soil parameters. All analyses of

AET, fire and soil parameters were carried out using the geographical information system ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA).

Statistical analysis

The environmental variables and patterns in species richness were tested for spatial autocorrelation using Moran's *I* coefficients (Legendre & Legendre 1998) for nine distance classes (Table 1). The distance ranges covered by the different distance classes varied in order to hold an equal number of observations in each distance class. The distances are based on the geographical distances between the centroids of the protected area polygons. Although spatial autocorrelation for most variables is low (i.e. mostly below 0.4), all variables except CEC showed significant spatial autocorrelation in at least one distance class. We therefore used statistical analyses that correct for spatial autocorrelation using the program Spatial Analysis in Macroecology (Rangel *et al*. 2006). Evaluation of the correlation coefficients between the environmental variables (Table 2) showed that CEC, soil carbon and nitrogen are highly correlated. Since soil nitrogen is directly related to vegetation quality (Breman & De Wit 1983), we took total nitrogen as the only parameter of soil fertility in the multiple regression and ordination analyses (see below).

We first explored the relationships between species richness and the environmental variables using univariate regression techniques. Species richness in the protected areas was then related to fire density, AET and soil fertility using both ordinary least squares (OLS) multiple regression and simultaneous autoregression (SAR). In contrast to conventional OLS regression, SAR models correct for spatial autocorrelation by taking not only the predictor variables into account but also the response values at neighbouring locations (Kissling & Carl 2008). Regression analyses were done for the entire species set as well as for the two main guilds, i.e. grazers and browsers/frugivores. Based on the results of the univariate regression, we tested both linear and polynomial multiple regression models in order to incorporate any quadratic terms. Three models were explored, using: (1) linear terms for all variables, (2) a quadratic term for AET, and (3) quadratic terms for both AET and fire. The best of these three models was then selected using partial F statistics (Quinn & Keough 2002) based on differences in the explained variance (sum of squares) of each model. These tests were performed on the OLS regression only.

Table 1. Spatial autocorrelation of the environmental variables and the distribution of ungulates over the 37 protected areas. Values refer to Moran's *I* coefficients with associated significance levels (* P < 0.05, ** P < 0.01). The upper bounds of the distance classes (in km) are given in parentheses in the first column. AET: actual evapotranspiration; CEC: cation exchange capacity; C: soil carbon; N: soil nitrogen.

Distance class	**AET**	**Fire**	**CEC**	**Total C**	**Total N**	**Grazers**	**Browsers, frugivores**	**All spp.**
1 (435)	0.342**	0.343**	0.005	0.052	0.140	0.276**	0.405**	0.245*
2 (689)	0.365**	-0.169	-0.156	0.114	0.163	-0.153	0.381**	0.117
3 (920)	0.063	-0.225*	-0.084	0.070	0.046	-0.331*	0.042	-0.166
4 (1144)	0.100	-0.111	-0.028	-0.111	-0.058	-0.015	-0.033	0.072
5 (1359)	-0.172	-0.008	0.094	-0.094	-0.175	0.078	-0.291	-0.147
6 (1607)	-0.067	0.093	-0.015	-0.191	-0.261*	0.021	-0.139	-0.037
7 (1942)	-0.069	-0.088	-0.053	-0.217*	-0.367**	-0.120	-0.058	-0.174
8 (2429)	-0.306*	-0.146	-0.065	-0.009	0.079	-0.081	-0.132	-0.141
9 (3939)	-0.517**	0.056	0.052	0.138	0.184	0.064	-0.436**	-0.022

The relation between the environmental variables and the composition of ungulate assemblages was assessed using a two-fold approach. First, differences in species composition (beta diversity) were related to differences in fire density, AET and soil fertility using partial Mantel tests (Legendre & Legendre 1998). The partial Mantel tests calculated the correlation between two distance matrices while controlling for the effects of geographical distances listed in a third matrix. Dissimilarity of species composition was quantified by Sørensen's (Bray–Curtis qualitative) index for presence–absence data. Distance matrices for the explanatory variables were based on Euclidean distances. Although partial Mantel tests provide a robust analysis of whether distance matrices are related, these tests cannot be used to partition the variability in species composition into fractions explained by each of the predictor variables (Borcard *et al.* 1992). Therefore partial redundancy analyses (RDA; Lepš & Šmilauer 2003) were carried out to assess the contribution of each environmental variable to ungulate assemblage composition. RDA is a linear ordination technique similar to the widely used principal

Table 2. Pearson's correlation coefficients (r) between actual evapotranspiration (AET), fire density, cation exchange capacity (CEC), and soil carbon and nitrogen, with associated significance levels based on Dutilleul's (1993) correction for spatial autocorrelation. *** P < 0.001.

	Fire	**CEC soil**	**Soil carbon (C)**	**Soil nitrogen (N)**
AET	0.194	-0.047	0.324	0.352
Fire		0.322	0.224	0.208
CEC soil			0.707***	0.687***
Soil carbon (C)				0.806***

components analysis, but where the latter extracts patterns from all variation (both explained and unexplained) in the species data, in RDA the variability in species composition is constrained by the variability in the environmental variables (Lepš & Šmilauer 2003). In other words, RDA only considers that part of the variability in species composition that can be explained by the predictor variables. Space was included as a predictor variable by means of a principal coordinates of neighbour matrices (PCNM) analysis (Borcard & Legendre 2002). In this technique a principal coordinates analysis was computed of a matrix containing the geographical distances between the protected areas, after which the principal coordinates were used as explanatory variables in the RDA. Variance partitioning of the environmental and spatial components that predict ungulate assemblage composition was done following Borcard *et al.* (1992) and Legendre (2007). The RDA analyses were carried out using the program Canoco (Ter Braak & Šmilauer 2002).

7.3 RESULTS

The univariate regression showed a quadratic relationship between AET and the species richness of grazers (Fig. 2a), but a linear relation with browsers (Fig. 2b). The relationship between fire and grazers could be described by either a linear or a quadratic curve (Fig. 2c), but there was no relation between fire and the species richness of browsers (Fig. 2d). Soil nitrogen did not significantly correlate with the species richness of grazers (linear: $R^2 = 0.03$, $P = 0.32$; quadratic: $R^2 = 0.15$, $P = 0.07$). The relation between soil nitrogen and

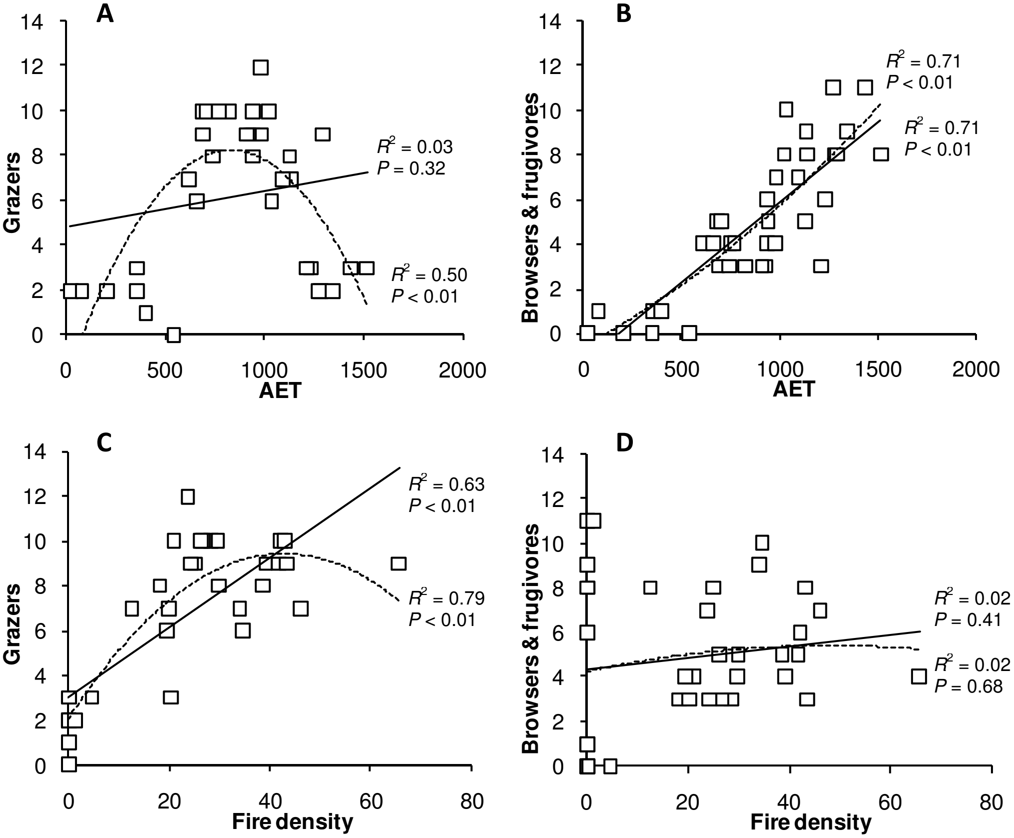

Fig. 2. Species richness of grazers (a,c) and browsers and frugivores (b,d) related to actual evapotranspiration (AET) (a,b) and fire density (c,d). The solid trendlines are based on linear regression, the dashed lines on quadratic regression. R square values and significance levels are shown for each regression line. AET is expressed in mm year^{-1} and fire density as the average annual percentage of the area covered by fire pixels (see text for details).

browsers was weak but significant (linear: R^2 = 0.13, P = 0.03; quadratic: R^2 = 0.30, P < 0.01).

In the multiple regression models (Table 3), the species richness of grazers was best described using a regression model that included quadratic terms for both AET and fire (R^2 = 0.79). This model fitted the data significantly better than an all linear model (R^2 = 0.63; F = 23.42, P < 0.01) or a model with a quadratic term for AET only (R^2 = 0.69; F = 15.69, P < 0.01). For browsers, the fit of the all linear model (R^2 = 0.72) was not significantly different from that of the models including quadratic terms for AET (R^2 =

Table 3. Multiple linear regression analysis relating the species richness of grazers and browsers + frugivores to actual evapotranspiration (AET), fire density and soil nitrogen. Coefficients ± standard error and t–test with associated significance levels are given for both ordinary least-squares (OLS) regression and simultaneous autoregression (SAR). Quadratic terms for AET and fire are listed as AET^2 and $Fire^2$, respectively. For details on model selection see text.* P <0.05, ** P < 0.01, *** P < 0.001.

Variable	**OLS**		**SAR**	
	Coefficient ± SE	***t***	**Coefficient ± SE**	***t***
Grazers:				
Constant	1.600 ± 1.276	1.254	1.661 ± 1.207	1.376
AET	0.003 ± 0.004	0.669	0.003 ± 0.004	0.717
AET^2	<-0.01 ± 0.000	-0.668	<0.001 ± <0.001	-0.689
Fire	0.321 ± 0.056	5.699***	0.319 ± 0.051	6.275***
$Fire^2$	-0.004 ± 0.001	-3.961***	-0.004 ± <0.001	-4.335***
Soil nitrogen	-0.263 ± 0.916	-0.288	-0.381 ± 0.846	-0.451
R^2	0.792		0.790	
Browsers + frugivores:				
Constant	-1.830 ± 0.940	-1.946	-0.981 ± 1.131	-0.868
AET	0.007 ± 0.001	8.115***	0.007 ± <0.001	7.731***
Fire	-0.007 ± 0.017	-0.420	<0.002 ± 0.016	0.121
Soil nitrogen	0.978 ± 0.940	1.040	0.670 ± 0.867	0.773
R^2	0.716		0.661	
All species:				
Constant	5.079 ± 2.153	2.359*	5.359 ± 2.061	2.600*
AET	0.001 ± 0.007	0.157	0.002 ± 0.007	0.282
AET^2	<0.001 ± 0.000	0.659	<0.001 ± <0.001	0.632
Fire	0.346 ± 0.095	3.636***	0.335 ± 0.085	3.964***
$Fire^2$	-0.004 ± 0.002	-2.744**	-0.004 ± 0.001	-2.864**
Soil nitrogen	0.648 ± 1.545	0.420	-0.170 ± 1.417	0.120
R^2	0.663		0.652	

Table 4. Redundancy analysis (RDA) showing the percentages variability in assemblage composition that is explained by actual evapotranspiration (AET), fire density and soil nitrogen. The shared space–environment percentages listed in the first column were calculated by subtracting the non-spatial component (second column) from the total percentages (third column).

Variable	**Sharing a spatial component**	**Excluding spatial component**	**Total**
Grazers:			
AET	8.69	1.63	10.32
Fire density	33.98	4.41	38.39
Soil nitrogen	-1.22	2.59	1.37
Total	41.45	8.63	50.08
Browsers + frugivores:			
AET	24.51	2.65	27.16
Fire density	15.17	3.50	18.67
Soil nitrogen	0.69	0.81	1.50
Total	40.37	6.96	47.33
All species:			
AET	19.79	1.93	21.72
Fire density	22.59	3.52	26.11
Soil nitrogen	0.39	1.54	1.93
Total	42.77	6.99	49.76

0.73; $F = 1.24$, $P = 0.27$) or both AET and fire ($R^2 = 0.73$; $F = 1.83$, $P = 0.19$). For the overall species set, including a quadratic term for AET did not significantly improve model fit compared to an all linear model (both $R^2 = 0.58$; $F = 0.37$, $P = 0.55$). However, including quadratic terms for both AET and fire resulted in significantly better model fit ($R^2 = 0.66$) compared to the linear model ($R^2 = 0.58$; $F = 7.97$, $P < 0.01$) or the model with a quadratic term for AET only ($R^2 = 0.58$; $F = 7.53$, $P = 0.01$). In contrast to the univariate regression, both the OLS and SAR multiple regression models identified fire density as the only significant variable explaining the species richness of grazers and the entire species set, whereas AET was the only significant variable explaining species richness of browsers/frugivores (Table 3). Soil nitrogen did not significantly predict species richness for any of the guilds or the whole species set.

The partial Mantel tests showed that ungulate beta diversity was significantly correlated with AET ($Z = 0.75$, $P < 0.01$), fire density ($Z = 0.39$, $P < 0.01$) and soil nitrogen ($Z = 0.15$, $P < 0.05$). No significant correlation could be found between species dissimilarity and soil cation exchange capacity ($Z = 0.01$, $P = 0.41$) or soil carbon content ($Z = 0.09$, $P = 0.21$). Fire density, AET and soil nitrogen together explained 46 to 51% of the variation in assemblage composition (Table 4). Fire density was the most important variable explaining assemblage composition of the overall species set (26%) and of grazers (38%), whereas the assemblage composition of browsers and frugivores was explained mostly by AET (27%). Soil nitrogen explained no more than 1 to 2% of the variation in assemblage composition. The environmental variables combined with spatial patterns explained 87 to 89% of ungulate beta diversity, of which 37 to 42% consisted of a purely spatial component (Fig. 3).

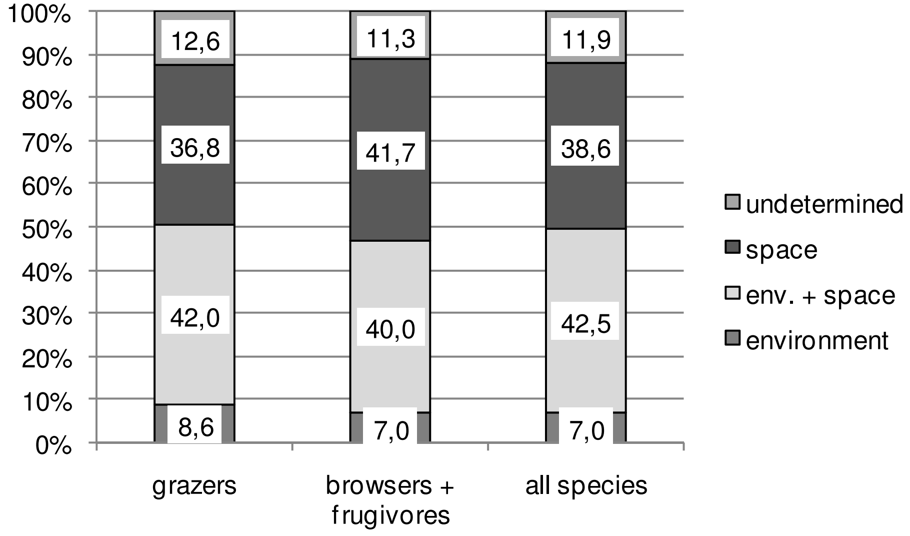

Fig. 3. Variance partitioning of ungulate assemblage composition into purely environmental, environmental plus spatial, purely spatial, and undetermined fractions.

7.4 DISCUSSION

Environmental factors

Olff *et al.* (2002) argued that diversity patterns of large mammalian herbivores are governed by gradients of plant abundance and quality, which in turn depend on moisture and nutrient availability (Breman & De Wit 1983). The idea that the nutritive quality of plants is a major determinant of the spatial distribution of populations of ungulates is not new, and various studies have shown that populations of herbivores track high-quality grass swards (e.g. Fryxell & Sinclair 1988, McNaughton 1988, 1990, Ben-Shahar & Coe 1992, Seagle & McNaughton 1992). However, our results suggest that in West African savannas anthropogenic fires override the effects of climatic and edaphic factors on the diversity of grazing herbivores by modifying both the quality and biomass of the grass sward.

Obviously, fires do not affect the ungulate community in areas where the limited herbaceous biomass cannot sustain grass fires, i.e. north of 13–15° latitude and in the wet forest zone. In arid zones with an annual rainfall below 300 mm grass production is limited by water rather than nutrient availability (Breman & De Wit 1983), resulting in a much higher forage quality than in the southern Sahel or moist savanna zones. Populations of grazing herbivores in the Sahelo-Saharan zone are thus likely to be constrained by quantity of forage rather than its quality. In contrast, going south of the savanna into the forest zone the grass layer is replaced by a continuous tree layer, resulting in a herbaceous food resource that is low in both biomass and quality (Prins & Olff 1998). As a result of these patterns, the species richness of grazers shows a unimodal pattern as a function of moisture availability (Fig. 2a). Grazers attain maximum species richness at AET values of 700–800 mm (Fig. 2a), corresponding to annual precipitation values of 1300–1400 mm. A similar pattern was shown by Prins & Olff (1998) on a continental scale. Based on both theoretical models of the relationship between precipitation and grass quality (Breman & De Wit 1983, Olff *et al.*, 2002) and on measurements of grass quality in the Guinean savanna (Klop *et al.* unpublished data), it seems surprising to find the maximum number of grazer species in latitudes where the quality of dry season grass is generally below herbivore maintenance levels. These patterns illustrate the colonization of the Guinean savanna by grazing herbivores, which in the absence of fires would transform into dense woodland or forest thickets (Swaine *et al.* 1992, Bond & Keeley 2005). However, whether and to what extent fires have pushed the grazer diversity peak southwards can only be guessed at, since testing such a hypothesis would require a direct comparison with West African savanna areas that have historically and currently never been burned, which to our knowledge do not exist. Our results show that the species richness of grazers in high-rainfall savanna areas such as Mbam Djerem or Outamba Kilimi is generally lower than in the northern Guinean savanna where moisture availability is lower. Even though fire is common in the southern Guinean savanna, the grass quality in these areas may be too low to support a high species richness of grazing herbivores.

Surprisingly, the quadratic relationship between grazers and AET shown by the univariate regression is not significant in the multiple regression model. Compared to a linear model, including a quadratic term for AET significantly improved model fit ($F = 22.55$, $P < 0.05$) with a significant relation between AET and grazer species richness ($P < 0.05$). However, when a quadratic term for fire is also included, the AET–grazer relationship is no longer significant. This illustrates the difficulties in comparing these different regression models where the terms are either linear or polynomial. Although the grazer–fire relationship can be described by either a linear or a quadratic term, the pattern shown in Fig. 2c suggests that it could also be fitted by an asymptotic curve. For example, a logarithmic or a power function fits these data equally well as a quadratic curve ($R^2 = 0.79$, $P = 0.00$), suggesting that the species richness of grazers levels off at high fire densities. This may be the result of changes in nutrient availability, since repeated burning can lead to net losses of soil organic matter and decreased nitrogen availability (Fynn *et al.* 2003). However, the long-term effects of burning on nutrient availability are variable and depend on various aspects of the fire regime such as seasonality and the type of fire.

In contrast to grazers, the species richness of browsers and frugivores increases linearly with AET, and the highest number of species of browsers and frugivores is found in the wet forest zone (Fig. 2b) where browse is abundant. In these areas the ungulate assemblages are dominated by browsers that are not dependent on grass quality and that can exploit high-rainfall environments, for example by subsisting on fruits as duikers do. In addition to species richness, the assemblage composition of browsers and frugivores was also mostly explained by AET. Fires did not explain species richness of browsers (Fig. 2d) as the availability of browse in the desert and forest zones is generally independent of fire, although in the savanna zone the availability and establishment of woody saplings is affected by fires. Diversity patterns of browsers are likely to be constrained by forage biomass rather than quality, since the quality of browse usually remains above herbivore maintenance levels throughout the year (De Bie 1991).

Compared with tropical grasses, the foliage of woody plants generally has higher protein and mineral contents (Le Houerou 1980) and lower fibre contents, which makes browse better digestible than grasses (Duncan & Poppi 2008). However, secondary compounds such as tannins are largely absent in grasses but generally abundant in browse (Duncan & Poppi 2008).

In contrast to Olff *et al*. (2002), we could not find a strong relationship between soil fertility and species richness of ungulates in West Africa. Soil nitrogen was significantly but weakly correlated with the species richness of browsers and with overall patterns in beta diversity, but only in the univariate regression, and it was not related to the species richness of grazers. In addition, the redundancy analyses showed that the contribution of soil nitrogen to assemblage composition was very small (i.e. around 1% for browsers and frugivores and 2% for grazers). Several studies have linked the distribution and biomass of African ungulates to nutrient availability (e.g. McNaughton 1988, 1990, Fritz & Duncan 1994, Olff *et al*. 2002), although soil nutrients need not always be related to nutrient levels in the vegetation (Ben-Shahar & Coe 1992). The lack of a strong relationship between soil fertility and species richness or assemblage composition is probably caused by a relatively homogeneous pattern of low soil fertility in our region compared with the variation in soil fertility on a global scale. It must be noted that apart from the Cameroon highlands and the Tibesti Massif in northern Chad, the West African region is largely void of volcanoes or large basaltic outcrops that, especially in East and southern Africa, have caused large regional differences in soil fertility. In addition, the importance of the relationship between soil fertility and grass quality for herbivore diversity patterns may be obscured by the large effects of fire on grass quality (Van de Vijver *et al*. 1999), as suggested by the non-significant relationships between soil nitrogen and species richness in the multiple regression models.

Spatial patterns

Much of the variation in assemblage composition that is explained by the environmental variables is spatially structured (Fig. 3). Not surprisingly, spatial structure is most evident in AET (Table 1). In addition to the shared environment–space components, pure spatial patterns account for major parts of the variability in assemblage composition. This spatial component may consist of environmental variables that were not incorporated into the analyses, any nonlinear relations between some variables (e.g. the AET–grazer relationship) or biological processes such as competition or dispersal (Legendre, 2007). Based on current knowledge of environment–herbivore relationships (East 1984, Fritz &

Duncan 1994, Olff *et al.* 2002), we do not think that we have missed any important environmental variables. However, the processes behind the purely spatial patterns warrant further study, and may include facilitation by other herbivores through the availability of high-quality forage on grazing lawns, or competition with cattle for grazing lands.

All environmental variables except CEC, and the patterns in species richness showed low but significant spatial autocorrelation. Spatial autocorrelation can be the result of various processes, including distance-related biological processes such as dispersal (Dormann *et al.* 2007) or dependence of the response variable upon some spatially structured explanatory variable (Legendre *et al.* 2002). The use of non-spatial regression models on such data may result in biased parameter estimates and poor model fit compared with spatially explicit models (Lennon 2000, Dormann 2007, but see Diniz-Filho *et al.* 2003, Hawkins *et al.* 2007). However, conventional OLS regression of our data gave comparable parameter estimates, standard errors, and model fit to the SAR model (Table 3). The similar outcomes of the OLS and SAR models are likely to be the result of the fact that spatial autocorrelation for most variables was low and mostly occurred in the short-distance classes (cf. Hawkins *et al.* 2007).

7.5 CONCLUDING REMARKS

Moisture and nutrient availability have been considered to be the most important determinants of the distribution and biomass of African ungulates (Fritz & Duncan 1994, Olff *et al.* 2002). In addition, our study demonstrates that regional diversity patterns of grazing herbivores are governed to a large extent by the widespread and mostly anthropogenic fires that are characteristic of the African savannas. Although fires only occur in areas with sufficient grass biomass and therefore also depend on moisture availability, our analyses show that moisture and nutrients alone fail to adequately predict the species richness of grazers in West Africa. This is in sharp contrast to the patterns of browsers and frugivores, for which species richness closely follows a gradient in productivity, and hence the availability of browse.

The review by Hawkins *et al.* (2003) shows that anthropogenic factors have received comparatively little attention in studies of broad-scale diversity patterns compared with energy- or waterrelated variables. Indeed, a quick search in the journals *Global Ecology and Biogeography*, *Diversity and Distributions* and *Journal of Biogeography* using the ISI Web of Knowledge learns that out of 874 articles on ‘species richness’ only

36 also relate to 'anthropogenic'. The results of this study highlight the importance of incorporating major human-induced disturbances or habitat alterations into analyses of diversity patterns.

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Appendix S1. The 37 protected areas covered by this study. The areas can be located on the map (Fig. 1) using the ID numbers. Latitude and longitude are for the area centroids and are given in decimal degrees. Mean values and standard deviation (SD) are given for the environmental variables. Area is expressed in km^2, actual evapotranspiration (AET) in mm year^{-1}, fire density in fire pixels year^{-1} km^{-2} (×100), cation exchange capacity (CEC) in cmol$_c$ kg^{-1}, soil organic carbon (C) content in g kg^{-1} and soil nitrogen (N) in g kg^{-1}.

ID	Country	Protected area	Lat	Lon	Area	AET	Fire density		Soil CEC		Soil C		Soil N	
							Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	Algeria	Tassili N'Ajjer	24.97	9.01	72000	20	0.00	0.00	11.98	3.61	9.02	5.40	0.88	0.50
2	Benin	Pendjari	11.23	1.53	2755	825	28.41	2.79	8.09	3.53	7.50	1.25	0.74	0.19
3	Benin, B. Faso, Niger	W	12.03	2.41	9570	689	26.77	2.29	8.69	5.38	7.40	2.38	0.72	0.24
4	Burkina Faso	Kabore Tambi	11.47	-1.26	2427	743	18.15	2.52	16.61	15.18	9.00	2.42	0.76	0.31
5	Burkina Faso	Sahel	14.50	-0.58	16000	544	0.00	0.01	7.69	6.76	4.99	2.28	0.58	0.25
6	Cameroon	Bénoué	8.35	13.83	1800	939	42.22	6.34	6.14	1.14	7.08	1.31	0.66	0.15
7	Cameroon	Korup	5.22	8.96	1260	1233	0.04	0.08	7.70	0.00	6.66	0.00	1.65	0.00
8	Cameroon	Mbam Djerem	5.85	12.77	4210	1139	12.55	0.86	6.73	0.88	11.49	2.31	0.95	0.19
9	Cameroon	Waza	11.29	14.70	1700	615	20.02	6.51	17.37	2.71	25.95	17.96	1.67	0.69
10	Chad	Ouadi Rime Ouadi Achim	15.52	19.25	80000	206	0.32	0.32	4.69	4.01	3.50	2.77	0.38	0.29
11	Chad	Zakouma	10.85	19.65	3000	749	20.97	4.77	9.91	7.58	6.56	1.64	0.63	0.14
12	Gambia	Kiang West	13.38	-15.92	110	661	19.55	12.97	10.57	0.00	12.27	0.00	1.33	0.00
13	Ghana	Bia	6.57	-3.07	78	1282	0.32	0.64	5.85	0.00	9.20	0.00	0.76	0.00
14	Ghana	Bui	8.46	-2.38	1821	1130	38.67	11.84	7.89	2.96	7.51	0.86	0.71	0.14
15	Ghana	Digya	7.43	-0.22	3126	1296	25.07	6.63	5.75	0.00	7.00	0.00	0.63	0.00
16	Ghana	Gbele	10.52	-2.19	565	941	65.75	6.29	13.76	3.53	12.94	2.50	1.20	0.32
17	Ghana	Kakum	5.45	-1.34	207	1346	0.00	0.00	5.85	0.00	9.20	0.00	0.76	0.00
18	Ghana	Mole	9.65	-1.76	4921	979	39.20	5.05	7.55	3.36	8.56	2.49	0.72	0.28
19	Guinea	Haut Niger	10.46	-10.17	722	943	29.95	6.59	6.57	0.00	10.60	0.00	0.80	0.00
20	Ivory Coast	Comoe	9.11	-3.73	11500	1024	43.03	10.79	8.87	3.86	8.74	0.77	0.86	0.16
21	Ivory Coast	Mont Sangbe	7.98	-7.25	950	1136	34.05	9.21	6.66	0.14	10.90	0.47	0.86	0.10

22	Ivory Coast	Tai	5.71	-7.13	3500	1434	0.03	0.04	6.68	0.14	10.97	0.48	0.88	0.10
23	Liberia	Sapo	5.39	-8.51	1308	1520	0.00	0.00	6.16	0.41	11.61	0.62	0.83	0.09
24	Mali	Ansongo Menaka	15.52	1.54	17500	357	0.10	0.04	3.39	2.39	2.59	1.53	0.30	0.17
25	Mali	Boucle du Baoule	13.87	-8.92	1878	687	41.82	4.38	7.31	0.82	5.16	0.57	0.57	0.06
26	Mali	Gourma	15.72	-2.77	1250	353	4.60	2.14	3.40	2.34	3.32	2.52	0.37	0.22
27	Niger	Air Tenere	19.27	9.60	77360	76	0.00	0.00	9.03	5.01	6.58	5.46	0.61	0.54
28	Niger	Gadabedji	15.14	7.15	760	400	0.13	0.26	6.20	7.27	5.21	6.07	0.47	0.46
29	Nigeria	Gashaka Gumti	7.48	11.71	6730	984	23.73	1.42	13.55	4.72	13.47	5.28	1.27	0.51
30	Nigeria	Kainji Lake	9.95	4.50	5340	927	43.50	7.96	7.58	2.97	8.76	2.68	0.85	0.33
31	Nigeria	Okomu	6.32	5.24	181	1213	20.30	11.87	11.97	1.95	12.75	0.66	1.30	0.04
32	Nigeria	Yankari	9.81	10.48	2240	771	29.74	9.09	10.05	2.08	11.63	2.56	1.26	0.27
33	Senegal	Niokolo Koba	13.01	-13.03	9130	705	26.24	7.61	13.45	3.75	12.00	3.06	1.17	0.29
34	Sierra Leone	Gola	7.47	-11.15	750	1276	1.30	1.10	10.48	4.03	14.00	0.32	1.22	0.11
35	Sierra Leone	Outamba Kilimi	9.77	-12.03	980	1036	34.71	3.98	11.48	4.08	13.92	0.16	1.25	0.11
36	Togo	Fazao Malfakassa	8.74	0.81	1920	1095	46.08	12.90	14.20	3.18	13.22	2.34	1.26	0.24
37	Togo	Keran	10.13	0.65	1700	911	24.28	0.85	6.79	2.75	7.13	0.36	0.68	0.13

Appendix S2. The 43 species of ungulates that occur, or that are known to have recently have gone extinct, in the 37 protected areas covered by this study. Taxonomy follows Duff & Lawson (2004). Body mass data (in kg) are from Kingdon (1997) and refer to the average weight of male and female, rounded to the nearest kg.

Common name	**Scientific name**	**Family**	**Guild**	**Body mass**
Addax	*Addax nasomaculatus*	Bovidae	Grazer	96
African buffalo	*Syncerus caffer*	Bovidae	Grazer	550
African forest elephant	*Loxodonta cyclotis*	Elephantidae	Mixed feeder	2150
African savanna elephant	*Loxodonta africana*	Elephantidae	Mixed feeder	4000
Barbary sheep	*Ammotragus lervia*	Bovidae	Mixed feeder	84
Bay duiker	*Cephalophus dorsalis*	Bovidae	Frugivore	20
Black duiker	*Cephalophus niger*	Bovidae	Frugivore	20
Black rhinoceros	*Diceros bicornis*	Rhinocerotidae	Browser	1050
Blue duiker	*Cephalophus monticola*	Bovidae	Frugivore	6
Bohor reedbuck	*Redunca redunca*	Bovidae	Grazer	47
Bongo	*Boocercus eurycerus*	Bovidae	Browser	277
Bushbuck	*Tragelaphus scriptus*	Bovidae	Browser	49
Common duiker	*Sylvicapra grimmia*	Bovidae	Browser	18
Dama gazelle	*Gazella dama*	Bovidae	Mixed feeder	58
Dorcas gazelle	*Gazella dorcas*	Bovidae	Generalist	18
Giant eland (Derby's eland)	*Taurotragus derbianus*	Bovidae	Browser	539
Giant forest hog	*Hylochoerus meinertzhageni*	Suidae	Grazer	179
Giraffe	*Giraffa camelopardalis*	Giraffidae	Browser	1340
Greater kudu	*Tragelaphus strepsiceros*	Bovidae	Generalist	210
Hartebeest	*Alcelaphus bucelaphus*	Bovidae	Grazer	161
Hippopotamus	*Hippopotamus amphibius*	Hippopotamidae	Grazer	1715
Jentink's duiker	*Cephalophus jentinki*	Bovidae	Frugivore	68
Klipspringer	*Oreotragus oreotragus*	Bovidae	Generalist	13
Kob	*Kobus kob*	Bovidae	Grazer	86
Korrigum / Tiang	*Damaliscus lunatus*	Bovidae	Grazer	126
Maxwell's duiker	*Cephalophus maxwellii*	Bovidae	Frugivore	8
Mountain reedbuck	*Redunca fulvorufula*	Bovidae	Grazer	29
Ogilby's duiker	*Cephalophus ogilbyi*	Bovidae	Frugivore	17
Oribi	*Ourebia ourebi*	Bovidae	Grazer	17
Pygmy hippopotamus	*Hexaprotodon liberiensis*	Hippopotamidae	Grazer	228
Red river hog	*Potamochoerus porcus*	Suidae	Omnivore	80
Red-flanked duiker	*Cephalophus rufilatus*	Bovidae	Frugivore	10
Red-fronted gazelle	*Gazella rufifrons*	Bovidae	Mixed feeder	24
Rhim (Slender-horned) gazelle	*Gazella leptoceros*	Bovidae	Mixed feeder	16
Roan antelope	*Hippotragus equinus*	Bovidae	Grazer	261
Royal antelope	*Neotragus pygmaeus*	Bovidae	Browser	2
Scimitar-horned oryx	*Oryx dammah*	Bovidae	Grazer	138

Sitatunga	*Tragelaphus spekii*	Bovidae	Grazer	84
Warthog	*Phacochoerus africanus*	Suidae	Grazer	83
Water chevrotain	*Hyemoschus aquaticus*	Tragulidae	Frugivore	11
Waterbuck	*Kobus ellipsiprymnus*	Bovidae	Grazer	215
Yellow-backed duiker	*Cephalophus silvicultor*	Bovidae	Frugivore	63
Zebra duiker	*Cephalophus zebra*	Bovidae	Frugivore	18