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

Erik Klop and Herbert H. T. Prins

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.

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 (Andreæ, 1990), and anthropogenic fires are an important feature of the West African savanna (Fig. 1). Although areas are burnt 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 unburnt 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 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

Figure 1 Fires recorded in the study area in 2006 based on Modis satellite observations (Justice et al., 2002). The scattered dots depict the fire pixels, each of which represents an area of approximately 1 km² 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, Benoue; 7, Korup; 8, Mbam Djereem; 9, Waza; 10, Ouadi Rime Ouadi Achim; 11, Zakouma; 12, Kiang West; 13, Bia; 14, Bui; 15, Diga; 16, Gbele; 17, Kakum; 18, Mole; 19, Haut Niger (Mafou and Amana Forests); 20, Comoe; 21, Mont Sangbe; 22, Tai; 23, Sapo; 24, Ansongo Menaka; 25, Boucle du Baoule; 26, Gourma; 27, Air Tenere (including the 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.
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?

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 cross-checked 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’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 km².

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 km² = 3100 km² at the equator) from a digital map (http://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; http://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 5 × 5 arcmin (equalling about 9.3 × 9.3 km = 86 km² at the equator). The following soil parameters were used: cation exchange capacity (CEC; in cmol 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
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. The upper bounds of the distance classes (in km) are given in parentheses in the first column.

<table>
<thead>
<tr>
<th>Distance class</th>
<th>AET</th>
<th>Fire</th>
<th>CEC</th>
<th>Total C</th>
<th>Total N</th>
<th>Grazers</th>
<th>Browsers + frugivores</th>
<th>All species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (435)</td>
<td>0.342**</td>
<td>0.343**</td>
<td>0.005</td>
<td>0.052</td>
<td>0.140</td>
<td>0.276**</td>
<td>0.405**</td>
<td>0.245*</td>
</tr>
<tr>
<td>2 (689)</td>
<td>0.365**</td>
<td>-0.169</td>
<td>-0.156</td>
<td>0.114</td>
<td>0.163</td>
<td>-0.153</td>
<td>0.381**</td>
<td>0.117</td>
</tr>
<tr>
<td>3 (920)</td>
<td>0.063</td>
<td>-0.225*</td>
<td>-0.084</td>
<td>0.070</td>
<td>0.046</td>
<td>-0.331*</td>
<td>0.042</td>
<td>-0.166</td>
</tr>
<tr>
<td>4 (1144)</td>
<td>0.100</td>
<td>-0.111</td>
<td>-0.028</td>
<td>-0.111</td>
<td>-0.058</td>
<td>-0.157</td>
<td>0.078</td>
<td>-0.291</td>
</tr>
<tr>
<td>5 (1359)</td>
<td>-0.172</td>
<td>-0.008</td>
<td>0.094</td>
<td>-0.094</td>
<td>-0.175</td>
<td>-0.157</td>
<td>0.078</td>
<td>-0.291</td>
</tr>
<tr>
<td>6 (1607)</td>
<td>-0.067</td>
<td>0.093</td>
<td>-0.015</td>
<td>-0.191</td>
<td>-0.261*</td>
<td>0.021</td>
<td>-0.139</td>
<td>-0.037</td>
</tr>
<tr>
<td>7 (1942)</td>
<td>-0.069</td>
<td>-0.088</td>
<td>-0.053</td>
<td>-0.217*</td>
<td>-0.367**</td>
<td>-0.120</td>
<td>-0.058</td>
<td>-0.174</td>
</tr>
<tr>
<td>8 (2429)</td>
<td>-0.306*</td>
<td>-0.146</td>
<td>-0.065</td>
<td>-0.009</td>
<td>0.079</td>
<td>-0.081</td>
<td>-0.132</td>
<td>-0.141</td>
</tr>
<tr>
<td>9 (3939)</td>
<td>-0.517**</td>
<td>0.056</td>
<td>0.052</td>
<td>0.138</td>
<td>0.184</td>
<td>0.064</td>
<td>-0.436**</td>
<td>-0.022</td>
</tr>
</tbody>
</table>

*P < 0.05, **P < 0.01.

AET: actual evapotranspiration; CEC: cation exchange capacity; C: soil carbon; N: soil nitrogen.

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.

<table>
<thead>
<tr>
<th></th>
<th>CEC</th>
<th>Soil carbon (C)</th>
<th>Soil nitrogen (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET</td>
<td>0.194</td>
<td>0.324</td>
<td>0.352</td>
</tr>
<tr>
<td>Fire</td>
<td>0.322</td>
<td>0.622</td>
<td>0.806</td>
</tr>
<tr>
<td>CEC soil</td>
<td>0.707*</td>
<td>0.687*</td>
<td></td>
</tr>
<tr>
<td>Soil carbon (C)</td>
<td></td>
<td>0.806*</td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.001.

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.

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 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).

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 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 ($R^2 = 0.69; F = 15.69, P < 0.01$) 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 ($R^2 = 0.73; F = 1.24, P = 0.27$) 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 $R^2 = 0.78; F = 0.37, P = 0.55$). However, including quadratic terms for both AET and fire resulted in a significantly better model fit ($R^2 = 0.66$) compared with 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 47–50% 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 1–2% of the variation in assemblage composition. The environmental variables combined with spatial patterns explained 87–89% of ungulate beta diversity, of which 37–42% consisted of a purely spatial component (Fig. 3).

**DISCUSSION**

**Environmental factors**

Olff *et al.* (2002) argued that diversity patterns of large mammalian herbivores are governed by gradients of plant abundance and

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**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 AET² and Fire², respectively. For details on model selection see text.

<table>
<thead>
<tr>
<th>Variable</th>
<th>OLS Coefficient ± SE</th>
<th>OLS t</th>
<th>SAR Coefficient ± SE</th>
<th>SAR t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grazers:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>1.600 ± 1.276</td>
<td>1.254</td>
<td>1.661 ± 1.207</td>
<td>1.376</td>
</tr>
<tr>
<td>AET</td>
<td>0.003 ± 0.004</td>
<td>0.669</td>
<td>0.003 ± 0.004</td>
<td>0.717</td>
</tr>
<tr>
<td>AET²</td>
<td>&lt; -0.01 ± 0.000</td>
<td>-0.668</td>
<td>&lt; 0.001 ± &lt; 0.001</td>
<td>-0.689</td>
</tr>
<tr>
<td>Fire</td>
<td>0.321 ± 0.056</td>
<td>5.699***</td>
<td>0.319 ± 0.051</td>
<td>6.275***</td>
</tr>
<tr>
<td>Fire²</td>
<td>-0.004 ± 0.001</td>
<td>-3.961***</td>
<td>-0.004 ± &lt; 0.001</td>
<td>-4.335***</td>
</tr>
<tr>
<td>Soil nitrogen</td>
<td>-0.263 ± 0.916</td>
<td>-0.381</td>
<td>-0.846</td>
<td>-0.451</td>
</tr>
<tr>
<td>R²</td>
<td>0.792</td>
<td></td>
<td>0.790</td>
<td></td>
</tr>
<tr>
<td>Browsers + frugivores:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-1.830 ± 0.940</td>
<td>-1.946</td>
<td>-0.981 ± 1.131</td>
<td>-0.868</td>
</tr>
<tr>
<td>AET</td>
<td>0.007 ± 0.001</td>
<td>8.115***</td>
<td>0.007 ± &lt; 0.001</td>
<td>7.731***</td>
</tr>
<tr>
<td>Fire</td>
<td>-0.007 ± 0.017</td>
<td>-0.420</td>
<td>&lt; 0.002 ± 0.016</td>
<td>0.121</td>
</tr>
<tr>
<td>Soil nitrogen</td>
<td>0.978 ± 0.940</td>
<td>1.040</td>
<td>0.670 ± 0.867</td>
<td>0.733</td>
</tr>
<tr>
<td>R²</td>
<td>0.716</td>
<td></td>
<td>0.661</td>
<td></td>
</tr>
<tr>
<td>All species:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>5.079 ± 2.153</td>
<td>2.359*</td>
<td>5.359 ± 2.061</td>
<td>2.600*</td>
</tr>
<tr>
<td>AET</td>
<td>0.001 ± 0.007</td>
<td>0.157</td>
<td>0.002 ± 0.007</td>
<td>0.282</td>
</tr>
<tr>
<td>AET²</td>
<td>&lt; 0.001 ± 0.000</td>
<td>0.659</td>
<td>&lt; 0.001 ± &lt; 0.001</td>
<td>0.632</td>
</tr>
<tr>
<td>Fire</td>
<td>0.346 ± 0.095</td>
<td>3.636***</td>
<td>0.335 ± 0.085</td>
<td>3.964***</td>
</tr>
<tr>
<td>Fire²</td>
<td>-0.004 ± 0.002</td>
<td>-2.744***</td>
<td>-0.004 ± &lt; 0.001</td>
<td>-2.864***</td>
</tr>
<tr>
<td>Soil nitrogen</td>
<td>0.648 ± 1.545</td>
<td>0.420</td>
<td>-0.170 ± 1.147</td>
<td>0.120</td>
</tr>
<tr>
<td>R²</td>
<td>0.663</td>
<td></td>
<td>0.652</td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.05, **P < 0.01, ***P < 0.001.

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**Table 4** Redundancy analysis (RDA) showing the percentage 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).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Grazers:</th>
<th>Browsers + frugivores:</th>
<th>All species:</th>
</tr>
</thead>
<tbody>
<tr>
<td>AET</td>
<td>8.69</td>
<td>24.51</td>
<td>19.79</td>
</tr>
<tr>
<td>Fire density</td>
<td>33.98</td>
<td>15.17</td>
<td>22.59</td>
</tr>
<tr>
<td>Soil nitrogen</td>
<td>-1.22</td>
<td>0.69</td>
<td>0.39</td>
</tr>
<tr>
<td>Total</td>
<td>41.45</td>
<td>40.37</td>
<td>42.77</td>
</tr>
</tbody>
</table>

![Figure 3](image-url)
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 & Popp, 2008). However, secondary compounds such as tannins are largely absent in grasses but generally abundant in browse (Duncan & Popp, 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 incorpo-
rated 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 relation-
ships (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 autocorre-
ation. 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).

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 water-
related 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 ‘anthro-
pogenic’. 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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Diversity patterns of West African ungulates


SUPPORTING INFORMATION

The following supporting information is available for this article:

Appendix S1 The 37 protected areas covered by this study.

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.

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