Predicting grazer distribution with grass quality and quantity parameters

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TABLE OF CONTENTS

SUMMARY

Predicting species distribution is an important part of ecology. There are numerous factors influencing the distribution of herbivores in an ecosystem. The distribution of food resources within an ecosystem is an important explanatory factor for herbivore distribution. Hence, the distribution of grass quality and quantity parameters (GQQPs) could explain grazer distribution. The goal of this study is to (i) explore the possibility of predicting grazer distribution with grass quality and quantity parameters, making use of new statistical modeling techniques, (ii) explore which parameters have most influence on grazer distribution in the wet and the dry season and (iii) create resource maps for grazer species for practical purposes. The study area is the Greater Makalali Private Game Reserve (GMPGR), South Africa. Maps of GQQPs (grass species abundance, herbaceous biomass, grass species richness and herbaceous coverage) are created by relating field measurements with Landsat ETM+ bands and variables derived from a digital elevation model using Generalized Additive Modeling (GAM). The accuracy of the GQQP maps was not very high, which could be caused by the date the Landsat ETM+ image was taken. The GAM method proved to be a flexible and empirical method. In 2005 and 2006 sighting locations of grazers were recorded throughout the GMPGR. The maps of the GQQPs are used to predict zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) distribution in the wet and the dry season making use of Ecological Niche Factor Analysis (ENFA). By applying a quantile reclassification to the values of the GQQP maps, so that the GQQP values have a uniform distribution, the grazer distribution was reliably predicted for the wet season. Predicting grazer distribution in the dry season wasn't successful, which could be because other factors than the GQQPs determine the distribution in the dry season, or be a result of the sampling method of the grazer locations, or be caused by a possible change in the values of the GQQPs in the dry season. From the results of the ENFA, 'resource maps' were calculated that mapped the habitat suitability for the grazers. One of the findings is that the only factors positively influencing the distribution of both zebra and wildebeest in the wet season, is a high abundance of *Urochloa mossambicensis* and in lesser extent a high herbaceous biomass. All other GQQPs had a negative influence on grazer distribution, which could be because the environment a certain grass species grows in is of more influence on grazer distribution than the grazing value of the grass species. This study describes a method that is suited to obtain grazer resource preference in a specific area, but is less suited for studying the universal resource preference of a certain grazer. For wildlife and range management this method provides detailed information on the food selection of grazers within a certain area. The method simultaneously gives insight into grazer food preference and the spatial distribution of the preferred food resources in the area.

INTRODUCTION

Predicting species distribution is an important part of ecology. Methods for predicting species distribution are being developed increasingly (Franklin, 1995; Guisan & Zimmermann, 2000). These methods focus either on the prediction of vegetation distribution throughout an area (Franklin, 1995, Gelfand *et al*. 2005, Lehmann, 1998) or the computation of habitat suitability (HS) for certain animal species (Aspinall, 1992, Dettki *et al*. 2003, Hirzel *et al*. 2002, Maggini *et al*. 2002, Ortigosa *et al.,* 2000). In this study these two aspects of ecology are combined to explore the possibility of predicting grazer habitat suitability with grass quality and quantity parameter maps, making use of new statistical modeling techniques (Generalized Additive Models (GAM) and Ecological Niche Factor Analysis (ENFA) (see chapter 'Methods')). Factors influencing grazer distribution will be examined, including the possible seasonal change in these factors.

As a result a 'resource map' will be produced, depicting the resource suitability for the grazer species. A resource map is comparable to a HS map. Each pixel value in a HS map indicates how close the predictor values represented in that pixel (GQQPs) are to the ecological needs of the focal species (Hirzel, 2004). A pixel value in a resource map indicates how well the resources in that pixel correspond to the dietary needs of the focal species. In this study the term 'habitat suitability' is used to express the suitability of the food resources. Resource maps can be used for different purposes, e.g.:

- Calculate carrying capacity of an area,
- Pinpoint geographical locations for introducing species,
- Determine the suitability of an area for wildlife conservation,
- Determine measurements and locations for habitat manipulation to create more or less suitable areas for certain species,
- Point out areas in which the encounter probability of a species is high.

Factors influencing the food selection by grazers are the grazer's morphological parameters (Hartley, 1982), interspecific competition/facilitation (Arsenault &

Owen-Smith, 2002), grass species (Ben-Shahar & Coe, 1992, Taylor & Walker, 1978), fiber content of the grasses (Westoby, 1974), mineral concentrations of the grasses (Ben-Shahar & Coe, 1992; Bremen & De Wit, 1983; McNaughton & Georgiadis, 1986; Seagle & McNaughton, 1992), grass species richness (Ben-Shahar & Coe, 1992) and grass biomass (Wilmshurst *et al*., 2000). Many of the above factors are subject to seasonal changes, and therefore the food preference of grazers can change with season (Ben-Shahar & Coe, 1992; Hirst, 1975). Due to different biotic and a-biotic factors the above mentioned quality parameters (mineral concentrations and fiber content) can differ between grass species, but also within species (Mutanga *et al*. 2004). In this study the within species differences are left out of consideration, because arguably, herbivores tend to select their diet mainly by selecting certain grass species (Taylor & Walker, 1978). The abundance of certain grass species (Grass species abundance (GSA) (%)) could thus be one of the quality factors influencing grazer distribution. Furthermore the grass species richness (SR) will be an explanatory quality factor for grazer habitat selection. The grass quantity will be expressed in herbaceous biomass (HBM) ($g*m^{-2}$) and the herbaceous coverage (HC) (%). These grass quality and quantity parameters (GSA, SR, HBM and HC) will be abbreviated to GQQP. Seasonal changes in the preferences of grazers for certain GQQPs will be examined by exploring the GQQPs influencing grazer distribution in the wet and the dry season.

It appears that all factors influencing the grass quality or quantity interact in complex ways (Hirst, 1975; McNaughton, 1983). Biotic factors that influence grass quality and quantity are tree cover (Looringh van Beeck, 2005; Scholes & Archer, 1997; Weltzin & Coughenour, 1990;) and grazing by herbivores (Anderson & Talbot, 1965; Georgiadis & McNaughton, 1990). On a regional scale the main abiotic factor influencing grass quality and quantity is the climate and soil fertility (Olff *et al.* 2002). However, at a local scale slope, position on slope (curvature), altitude, aspect, soil characteristics and fire are of more importance

(Anderson & Talbot, 1965; McNaughton, 1983; Mutanga *et al*., 2004; Perez Corona *et al*., 1994; Perez Corona *et al*., 1998).

Slope, aspect, curvature and altitude can be derived from a digital elevation model (DEM). Other factors influencing the GQQPs have shown to be correlated to digital numbers of multispectral satellite images. The spectral bands of the multispectral satellite images (i.e. Landsat ETM+) are commonly used for the determination of different ecological variables or gradients, like differentiation of vegetation from soils, forest-type mapping (blue band), vegetation vigor (green band) chlorophyll absorption level, plant species differentiation (red band), biomass estimation (near infrared band), mineral and rock type discrimination and vegetation and soil moisture levels (middle infrared band) (Kerr & Ostrovsky, 2003; Lillesand *et al.*, 2004). Everitt *et al*. (1989) found the middle infrared band to be a good predictor for grassland phytomass.

A commonly used derivative from the red and near infrared band is the Normalized Difference Vegetation Index (NDVI). Ecological variables that have been correlated with NDVI are percentage grass cover (Liu *et al*., 2004), species richness (Gould, 2000), biomass (Schino *et al.* 2003), leaf area index (Carlson & Ripley, 1997) and crown closure (Xu *et al.* 2003). Peterson (2005) modeled grass species cover with elevation data, the green Landsat band and a derivative of NDVI as significant predictor variables. Hence, digital elevation models and multispectral satellite images should be suitable for predicting the GQQPs.

The goal of this study is to (i) explore the possibility of predicting grazer distribution with grass quality and quantity parameters, making use of new statistical modeling techniques, (ii) explore which parameters have most influence on grazer distribution in the wet and the dry season and (iii) create resource maps for grazer species for practical purposes.

METHODS

Introduction

Figure 1 shows a flowchart of the methodological procedure used in this study. The first step of the procedure is to relate the GQQPs to the predictor variables derived from a Landsat ETM+ image and a DEM, making use of GAM. The second step is to relate sighting locations of grazers to the mapped GQQPs, making use of ENFA. The procedure will be thoroughly discussed per step in this chapter.

Study area

The study area is The Greater Makalali Private Game Reserve (GMPGR). This fenced private game reserve is situated in the Limpopo (Northern) Province of South Africa (between 24°03'S – 24°13'S and 30°31'E – 30°48'E). The reserve size is approximately 24.500 hectares (245 km^2) (Makalali research, 2005). The reserve started in 1993 with the purchase of 7.500 hectares (75 km^2) of cattle ranch and in 1994 the first game was reintroduced into the reserve (Looringh van Beeck, 2005). The vegetation in the GMPGR is classified as an arid Lowveld vegetation (Acocks, 2000), which is part of the savanna biome in South Africa (Low & Rebelo, 1996). The soils in the GMPGR area are minimally developed and usually shallow on hard or weathering rock. Lime is generally present in part or most of the landscape (Institute for Soil, Climate and Water, 2000). Annual rainfall is between the 440 and 560mm (Surface

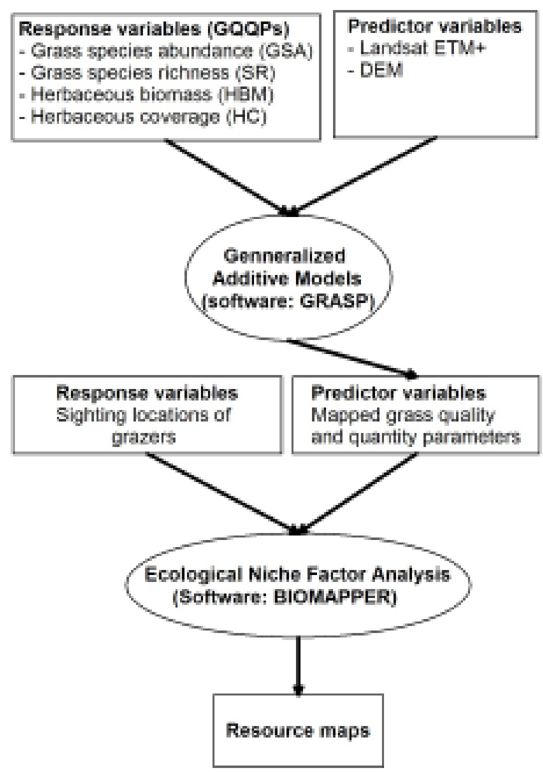

Figure 1: Flowchart of the methodological procedure used in this study. The first step of the procedure is to relate the GQQPs to the predictor variables derived from a Landsat ETM+ image and a digital elevation model (DEM), making use of Generalized Additive Modeling (GAM). The second step is to relate sighting locations of grazers to the mapped GQQPs, making use of Ecological Niche Factor Analysis (ENFA)

resources of South Africa, 1990). Most of the rain falls in the rain season, which is from November through April (Scholes, 1997). An extensive network of dirt roads cuts through the GMPGR.

The GMPGR is home to a rich variety of wildlife, among which a couple of grazers (Looringh van Beek, 2005; Makalali research, 2005). The two most abundant grazers are the Plains Zebra (*Equus burchelli*) and the Blue Wildebeest (*Connochaetes taurinus*). These two species are the grazers on which this study focuses, henceforth referred to as zebra and wildebeest respectively.

Since the sampling areas were determined prior to the research by using existing spatial datasets (see ‘Data acquisition’), the research area is restricted to the area that is covered by the forest type classification map (*Appendix 1*). This area covers approximately 12.500 hectares (125 km^2) of the reserve. This area was also used for model development.

Data acquisition

To make sure all environmental variables were sampled equally over the range of values, the sampling areas had to be defined *a priori* to the data acquisition. This can best be achieved by using random-stratified sampling (Guisan & Zimmermann, 2000; Hirzel & Guisan, 2002). Here the random-stratified sampling technique as described by Maggini *et al.* (2002) was used. Factors that have a potential influence on grass quality and quantity (slope, aspect, curvature and tree cover (see chapter ‘Introduction’)) were split into successive classes. A combination of all environmental classes defined the strata that had to be sampled equally. Information on the tree cover was obtained from a forest classification of the GMPGR by Druce (2000). *Table 1* shows the environmental classes used to define the strata. A total of 2 (slope) * 2 (aspect) * 3 (curvature) * 3 (tree cover) = 36 strata were used.

Table 1
Classes of environmental factors used to define the strata for random-stratified sampling

Environmental factor	**Classes**		
Slope	Flat (1-3 degrees)		Steep (3-7 degrees)
Aspect	North (NE, N, NW)		South (SE, S, SW)
Curvature	Convex (-1,9 - -0,025)	Flat (-0,025 – 0,025)	Concave (0,025 – 3,1)
Tree Cover	Grassland	Open Woodland	Closed Woodland

With ArcGIS (ESRI, 2004) all suitable potential sampling areas were calculated, by selecting the areas with a minimum dimension of 50 by 50m. From these suitable areas a minimum of 200 sampling areas were selected by hand (Evans & Love, 1957), so that all strata were more or less equally sampled and there was an even distribution of the locations over the study area. There is a larger area of closed woodland compared to grassland and open woodland in the study area (*Appendix 1*) and because the distribution of the sampling areas had to be more or less equally distributed over the study area, the 3 different tree cover classes, grassland, open woodland and closed woodland, were sampled in a ratio 1:1:2 respectively. A minimum distance of 250m between sampling areas was used to prevent spatial autocorrelation. Autocorrelation arises when sampling areas are located so close to each other that there is no independence between the observations (Guisan & Zimmermann, 2000). For efficiency most plots were within 300m of roads, which are abundant in the GMPGR. The coordinates of the centre points of the sampling areas were then calculated.

For the fieldwork certain grass species were selected to give an even selection of species with a high and a low grazing value. The grass species selected were abundant grass species in the GMPGR (ARC, 2004). Five grass species have a high grazing value, six a low grazing value and three an average grazing value (Outshoorn, 1999) (*Table 2*). The grass species that proved to have an average abundance of lower than 4% were not included to predict grazer distribution, since it was considered unlikely that grass species with a very low abundance have a significant effect on grazer distribution.

The GSA and HC in each location were sampled making use of the step-point method (Evans & Love, 1957). With a 12 channel GPS receiver (Garmin® eTrex Summit) the centre point of the sampling area was located. A zigzag route was walked through the virtual rectangular area, making sure the distance to the centre point never exceeded 25m. Trees and woody thicket were by-passed. Every 4 steps the vegetation element in front of the observers foot was recorded, which was either one of the selected grass species (*Table 2*), 'other grass species' (all remaining grass species), 'forbs' (all other herbaceous vegetation that is not grass) or 'bare soil'. In every sampling area 100 recordings were done. The HC (%) per sampling area is calculated as all recordings (100) minus the 'bare soil' recordings. The SR is the number of grass species recorded in a sampling area, adding 1 if 'other grass species' are recorded. The category 'other grass species' can consist of various grass species. The SR is therefore the minimum number of species in a sampling area.

A total of 220 plots were sampled in the GMPGR during the wet season in March and April 2006. Eight plots were sampled twice, walking a different route, to estimate the accuracy of this sampling method. These locations were compared to each other making use of the similarity ratio of Sörensen (*Appendix 2*). This calculation showed that these locations have an average similarity of 79 % in contrast to randomly paired plots, which have an average similarity of 44 %. The step-point method was thus considered to be a fairly accurate technique in this research.

Table 2
Grass species sampled in this study

Latin name	English name	Abbreviation	Grazing value (Outshoorn, 1999)	Percentages (ARC, 2004)	Percentage (observed)
Urochloa mossambicensis	Bushveld signal grass	UROMOSAM	High	20,6%	28,2%
Digitaria eriantha	Common finger grass	DIGERIAN	High	17,0%	12,1%
Panicum maximum	Guinea grass	PANMAXIM	High	10,2%	10,6%
Eragrostis rigidor	(Broad) Curly leaf	ERARIGID	Average	7,5%	2,3%
Schmidtia pappophorides	Sand Quick	SCHPAPPO	High	7,3%	3,6%
Brachiaria deflexa	False signal grass	BRADEFLE	Average	6,3%	6,0%
Enneapogon sp. (E. Cenchroides & E. Scoparius)	nine-awned grass & bottelbrush grass	ENNEAPOG	Low	6,2%	5,8%
Aristida sp.	Three-awned grasses	ARISTIDA	Low	4,9%	5,7%
Bothriochloa radicans	Stinking grass	BOTRADIC	Low	4,3%	5,1%
Melinis repens	Natal Red Top	MELREPEN	Low	4,1%	3,5%
Pogonarthria squarrosa	Herringbone grass	POGSQUAR	Low	2,7%	1,4%
Heteropogon contortus	Spear grass	HETCONTO	Average	2,1%	2,7%
Themeda triandra	Red grass	THETRIAN	High	1,4%	0,9%
Cymbopogon plurinodes	Narrow-leaved turpentine grass	CYMPLURI	Low	1,3%	4,5%
			Total:	95,7%	92,3%

To measure the HBM a disk pasture meter (polystyrene plate: 45 x 45cm, 956g) was used (Harmoney *et al*. 1997; Michalk *et al*., 1999; Sanderson *et al*. 2001). Every 3 recordings taken with the step-point sampling a disk-measurement was taken, which totaled to 33 measurements per sampling area, which is sufficient to estimate HBM (Michalk *et al*., 1999; Rayburn & Lozier, 2003). The disk pasture meter isn't suitable for measuring woody vegetation biomass (Michalk *et al.* 1999). Attention was paid that no woody species were present under the disk when taking the measurements. However, forbs were not avoided, because they were often intermingled with grasses.

To calibrate the disk pasture meter readings, 94 disk-measurements were followed by clipping and weighing the grass under the disk to estimate the HBM (Dörgeloh, 2002). The disk pasture meter is affective for both dry weight (Dörgeloh, 2002; Rayburn & Lozier, 2003) and fresh weight (Michalk *et al.* 1999) biomass measurements. Here fresh weight was chosen to express the HBM. A regression model was developed to quantify the conversion factor from disk-height to HBM ($g*m^{-2}$).

Grass quality and quantity parameter predictions

To eventually relate grazer distribution to GQQPs, the GSA, SR, HC and HBM needed to be mapped. In order to do this a predictive vegetation model needed to be formulated. A predictive vegetation model predicts the geographic distribution of vegetation composition across a landscape from mapped direct or indirect environmental variables (Franklin, 1995; Guisan & Zimmermann, 2000). The model that was suitable for this study is an empirical model, based on indirect predictive variables (Guisan & Zimmermann, 2000). Generalized regression models relate response variables (GQQPs) to a combination of environmental predictors (Landsat ETM+ bands, NDVI and DEM derivatives). Several regression models exist, but the most flexible and empirically based regression model is the generalized additive model (GAM). A GAM implements non-parametric 'smoothers' in regression models to each environmental predictor individually and calculates the response variable's response to obtain a fitting model (Guisan & Zimmermann, 2000). A GAM determines the shape of the response curve from the data instead of *a priori* determined parametric responses (Lehmann, 1998). Since this study was designed to model grass quality and quantity distribution in the GMPGR for consumption by grazers, a GAM is a suitable procedure to apply to the model.

GRASP (Generalized regression analysis and spatial predictions) is a freeware statistical software package that assists in spatial predictions making use of GAMs. GRASP is suited for predicting species distributions (Lehman *et al*., 2002). This software was used to analyze the data.

The predictor variables used to calculate the spatial predictions of the GQQPs were derived from a digital elevation model (DEM) (Hole-filled seamless SRTM data V1, 2004) and a cloud free Landsat 7 ETM+ image from 21st May 2001 (Landsat 7 ETM+ images, 2001) (*Table 3*). The DEMs from the SRTM mission have an absolute height error and absolute geolocation error of less than 12m for 90% of the data (Rodriguez *et al*. 2005). The Landsat 7 ETM+ image has an absolute positional accuracy of 50m RMS. The Normalized Difference Vegetation Index (NDVI) was calculated from band 3 and 4 (Kerr & Ostrovsky, 2003):

Table 3
Predictor variables used to calculate the GQQPs with GAMs. All predictors are derived from either a DEM or a Landsat ETM+ image. The maximum spatial resolution is 90 m.

Source	Variable	Code	Spatial resolution (m)
DEM	Slope	PRSLODEM	90
	Aspect	PRASPDEM	90
	Curvature	PRCRVDEM	90
	Altitude	PRHGTDEM	90
Landsat ETM+	Band 1	SATNN10	28,5
	Band 2	SATNN20	28,5
	Band 3	SATNN30	28,5
	Band 4	SATNN40	28,5
	Band 5	SATNN50	28,5
	Band 7	SATNN70	28,5
	Band 8	SATNN80	15
	NDVI	SATNDVI	28,5

NDVI = (band 4 – band 3)/(band 4 + band 3)

Although a forest classification was available of the GMPGR (Druce, 2000) (*Appendix 1*), this dataset was not used as a predictor variable, because it is more generalized than the Landsat image and the Landsat image is of a more recent date.

A forward, stepwise model selection was applied, making use of an ANOVA F-test (p = 0,05) for quasi models to select the significant predictor variables that were used in the GAM analysis. The quasi model was selected because it is used for under- or over- dispersed binomial and poisson models (Lehman *et al*. 2004). Correlation between the predictor variables was calculated and the maximum correlation set to 0,85 (R^2 = 72 % correlated). GRASP removes predictors that have a too high correlation from the analysis prior to model formulation. All predictors were smoothed with 4 degrees of freedom.

GRASP-derived models were validated by comparing the predicted values with the actual values. Besides that a cross-validation was done, by randomly splitting the predictor dataset into 5 identically-sized groups (default value). The model was recalculated, leaving out one group at a time. Predictions were made for the omitted group. The correlation between predicted and observed values was calculated for Poisson and normally distributed data and the ROC (area under curve) test was used for binomial data. The cross-validation gives an indication of the stability of the model (Lehman *et al*. 2002; Lehman *et al*. 2004).

Grazer sighting locations

In 2005 and January through April 2006 locations of grazer sightings were collected in the GMPGR. The observations were done by an often changing group of volunteers, who drove through the GMPGR in the early morning and/or late afternoon on an almost daily basis. Grazer sightings were also recorded on weekly walks through the GMPGR. Making use of detailed maps or GPS receivers the ground location of the observer was recorded, and the distance to the grazer estimated. For this study sightings were selected that have a maximum estimated distance of 100m between grazer and observer. The grazer sighting locations were spilt up into a dataset for the dry season (i.e. June through September 2005) and for the wet season (i.e. January through April 2005 and November through April 2006) (Scholes, 1997). This resulted in 296 sightings for wildebeest in the wet season and 116 in the dry season, and for zebra 432 in the wet and 176 in the dry season.

Resource maps

To predict areas that are preferred by grazers a model was needed that links the grazer sightings with the GQQP maps. Since there was only grazer presence data available and no information on areas where no grazers occur, a model that worked with presence data only was needed. An option was to use a GAM with 'pseudo-presence' points, but this method is sensitive to errors, especially when working with species that are common in the study area (Pearce & Boyce, 2006). Therefore the choice was made for the method of Ecological Niche Factor Analysis (ENFA) (Hirzel *et al*. 2002). ENFA is a reliable method that gives good results with a low sample size and an average data quality (Hirzel *et al*. 2001)

"ENFA computes habitat suitability models by comparing grazer distribution in the GQQP space with the GQQP distribution over the whole range of values. The analysis summarizes al the information in a couple of ecologically meaningful standardized and uncorrelated factors, similar to Principal Component Analysis. The first factor calculated with ENFA is the marginality factor, which indicates how much the species' habitat deviates from the mean available habitat. The following factors indicate the sensitivity of the species to deviations from the optimal values of the concerning variable." (paraphrased after Hirzel *et al*. 2002) For each factor the frequency distribution and median is calculated and mapped. The HS can be computed making use of four algorithms: median, distance geometric mean, distance harmonic mean, minimum distance (Hirzel & Arlettaz, 2003). These methods are incorporated in the freeware software package BIOMAPPER 3.2 (Hirzel *et al*. 2006), which was used for the calculation of the resource maps.

“The habitat suitability models are validated by splitting the dataset of grazer sighting locations into k identically sized groups. The HS model is computed k times, leaving out one group at a time (validation group), which results in k different HS maps. To evaluate the predictive power these maps are compared making use of the method as described in Boyce *et al*. (2002) (Boyce index). The k different HS maps are reclassified into 4 (default value) successive classes. Each class contains a proportion of the total area of the HS map (A) and a proportion of the locations in the validation group (N). If the model is reliable a monotonic increase is expected between classes with a low HS (having a low N/A ratio) and classes with a high HS (having a high N/A ratio). The Spearman rank correlation is used to measure the monotonicity of the increase, which results in the Boyce index. The Boyce index varies between -1 and 1. Values close to 1 indicates a reliable HS model. Values around 0 indicate a model that could be based on chance and negative values indicate an erroneous model.” (paraphrased after Hirzel, 2004). The number of partitions (k) was determined by Huberty’s rule (Huberty, 1994) implemented in BIOMAPPER 3.2 (In practice the number of partitions was always 4).

RESULTS

Herbaceous biomass measurement

The disk-pasture meter proved to be a quick and easy way to measure the HBM. To calibrate the meter a trendline was fitted through a scatterplot of the disk height and the HBM ($g*m^{-2}$) (*Appendix 3*). In some cases a square root or log linear transformation could give a better fit than a linear regression model (Dörgeloh, 2002). In this study the linear regression model has a better fit (R^2 = 0,651) than a log linear (R^2 = 0,601) or a square root (R^2 = 0,650) transformation of the HBM, so the HBM is computed as: HBM = 26,349*height (cm) for all sampling areas.

Grass quality and quantity parameter predictions

The GQQP maps were created using GRASP (Lehman *et al*. 2004). The correlation between the predictor variables (*Appendix 4*) shows a too high (> 0,85) correlation between Landsat band 2 (green), band 3 (red), band 5 (middle infrared) and band 7 (middle infrared). Therefore band 3 and band 7 are left out of the analysis. The significant predictor variables per GQQP and their response curves are shown in *Appendix 5*. From these significant predictor variables maps of the response variables are created (e.g. *Figure 2*)

For the GSA and HC maps a binomial distribution (continuous between 0 and 1) is selected; for the SR a poisson distribution and for the HBM a Gaussian distribution (Lehman *et al*. 2004). The results of the validation (*Table 4*) show an average validation of 0,56 for the GSA model, indicating that on average 33,4% (R^2) of the variation in GSA was explained by the model. The cross-validation value of 0,329 indicates a low stability of these models, but since the model doesn't have to be very general, this value is acceptable. The same counts for the HBM, HC and SR models. Interesting is that predictor NDVI accounts for 49% of variation in HBM, which is in accordance with Schino *et al.* (2003).

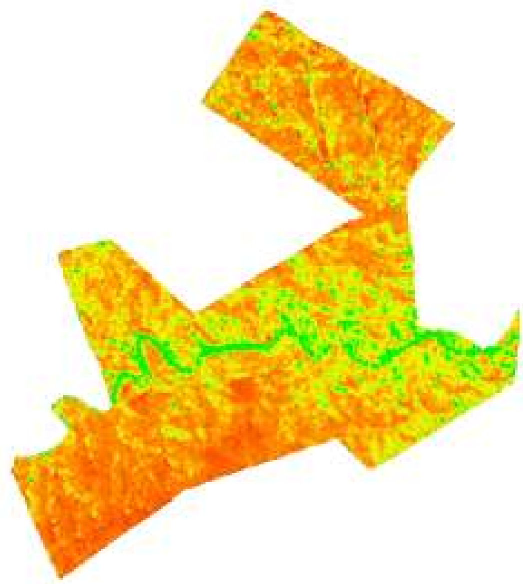

Figure 2: The abundance map of Panicum maximum in the GMPGR as predicted from the significant predictor variables altitude and Landsat band 5. The abundance ranges form high (green) to low (red).

As mentioned in 'Methods' the grass species with an average abundance of lower than 4% are left out of subsequent analysis. These omissions are also backed up by the fact that a majority of these grass species produced unreliable GSA maps. The GSA maps of *M. repens* and *H. contortus* have a low explained variation (<15%). The abundance maps of

T. triandra and *S. pappophoroides* have a very low model stability (cross-validation < 0,11). It is likely that these species abundances are not reliably predicted, because of a low sample size. The species abundance maps of *E. rigidor* and *P. squarrosa* are also left out of subsequent analysis (average abundance = 2,3% and 1,4 % respectively). The HC map is also excluded from subsequent analysis, due to a low explained variation (13%).

Table 4
Table of the validation and cross-validation of the GAMs calculated for each GQQP. The upper part of the table (above the line) shows the values of the grass species abundances and the average value. The bottom part (under the line) shows the values of the herbaceous biomass (HBM), Herbaceous coverage (HC) and grass species richness (SR). The GAMs are calculated in GRASP (Lehman et al., 2002). GRASP didn't calculate any cross-validation results when working with binomial distributions. A poisson distribution did give cross-validation results and since the validation results of a binomial and poisson distribution are as good as similar, the cross-validation results of a poisson distribution are used.

Response var.	Cross-validation	Validation	R^2	Significant Predictors	Abundance (observed)
Urochloa mossambicensis	*0,641*	0,743	0,552	NDVI, Landsat band 8, Landsat band 4, Height, Curvature, Slope	28,2%
Digitaria eriantha	*0,375*	0,430	0,185	Landsat band 4, Height	12,1%
Panicum maximum	*0,506*	0,548	0,300	Landsat band 5, Height	10,6%
Brachiaria deflexa	*0,223*	0,583	0,340	NDVI, Landsat band 5, Curvature, Aspect	6,0%
Enneapogon sp. (E. Cenchroides & E. Scoparius)	*0,499*	0,638	0,407	Landsat band 8, Landsat band 5, Landsat band 4, Aspect, Slope	5,8%
Aristida sp.	*0,320*	0,427	0,182	Landsat band 4, Height, Curvature	5,7%
Bothriochloa radicans	*0,338*	0,707	0,500	Landsat band 8, Landsat band 4, Landsat band 2, Height, Aspect	5,1%
Cymbopogon plurinodes	*0,367*	0,557	0,310	NDVI, Landsat band 4, Height	4,5%
Schmidtia pappophorides	*0,079*	0,605	0,366	Landsat band 5, Landsat band 1, Height, Curvature	3,6%
Melinis repens	*0,242*	0,304	0,092	Landsat band 4	3,5%
Heteropogon contortus	*0,170*	0,311	0,097	Landsat band 8, Aspect	2,7%
Eragrostis rigidor	*0,242*	0,561	0,315	NDVI, Landsat band 4, Landsat band 2, Height, Slope	2,3%
Pogonarthria squarrosa	*0,503*	0,627	0,393	NDVI, Height, Aspect	1,4%
Themeda triandra	*0,107*	0,802	0,643	NDVI, Landsat band 5, Landsat band 4, Height, Curvature	0,9%
Average	**0,329**	**0,560**	**0,334**		
Herbaceous biomass	0,193	0,701	0,491	NDVI	
Herbaceous coverage		0,364	0,132	Aspect, NDVI	
Grass species richness	0,356	0,494	0,244	Landsat band 5, Landsat band 8	

Resource maps

The output of the GAM (GQQP maps), with the omission of the HC map and the grass species with an average abundance lower than 4%, are used as input for the ENFA. To compute the HS model from the ENFA the number of factors was retained, so that at least 80 % of the total variance was accounted for. The wildebeest wet season dataset was used to test the models. The first ENFA was performed with the untransformed maps from the GAM, which produced bad results (Boyce index was not significant) for all 4 algorithms (median, distance geometric mean, distance harmonic mean, minimum distance) with the cross-validation of the HS model (*Table 5*). Normalizing the GQQPs with a Box-Cox transformation, like advised (Hirzel *et al*. 2002), resulted in erroneous GQQPs, that were too highly correlated, so the ENFA failed to compute. A visual analysis of the GQQPs showed that some GQQPs didn't have a normal distribution, mainly because of some extreme values, resulting from the GAM (e.g. *Figure 3*). A square root transformation, to extract the extreme values, didn't improve the quality of the HS model (*Table 5*). These extreme values have a disproportionate influence on the ENFA. To extract the extreme values a standard deviation reclassification of the GQQPs was performed in ArcGIS (ESRI, 2004). This classification didn't produce any reliable HS models (*Table 5*), possibly because some GQQPs were still skewed.

Table 5
Results of the cross-validation of the HS models for all 4 algorithms applied to the Wildebeest wet season dataset, produced in Biomapper 3.2 (Hirzel et al. 2006). The Boyce index indicates the model reliability. The Boyce index (first value) varies between -1 and 1. Values close to 1 indicates a reliable HS model. Values around 0 indicate a model that could be based on chance and negative values indicate an erroneous model. The second value is the significance of the Boyce index.

	Algorithm			
Data transformation	median	distance geometric mean	distance harmonic mean	minimum distance
None	0,75 +- 0,25	0,2 +- 0,5	0,45 +- 0,55	0,55 +- 0,45
Box-Cox	ENFA wasn't performed, due to very high correlation of tranformed EGVs			
Square root	0,55 +- 0,45	0,65 +- 0,35	0,65 +- 0,35	0,55 +- 0,45
Standard deviation reclassification (ArcGIS)	0,7 +- 0,41	0,25 +- 0,43	0,6 +- 0,32	0,8 +- 0,2
Quantile reclassification (ArcGIS)	0,25 +- 0,09	0,65 +- 0,30	1 +- 0	0,85 +- 0,09

Normality isn't formally required for the estimation of principal components and many procedures based on multivariate normality are robust to deviations from normality (Rencher, 2002). To not discard the extreme values and to flatten out the skewed GQQPs a uniform distribution of the GQQPs is examined. A quantile reclassification (ArcGIS (ESRI)) of the GQQPs into 10 equal sized categories produced fairly uniform distributions (e.g. *Figure 4*). The fact that the distribution is now made up of integer numerical values, should not cause irregularities for ENFA (Hirzel, 2004). This reclassification did produce reliable HS models (Boyce index = 1.0, $P < 0,05$), when making use of the distance harmonic mean algorithm (*Table 5*).

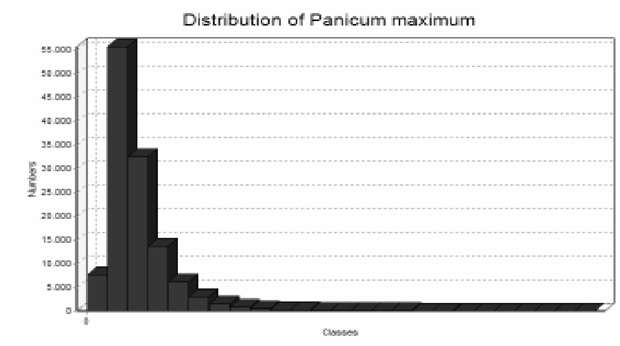

Figure 3: Distribution of Panicum maximum as predicted by the GAM.

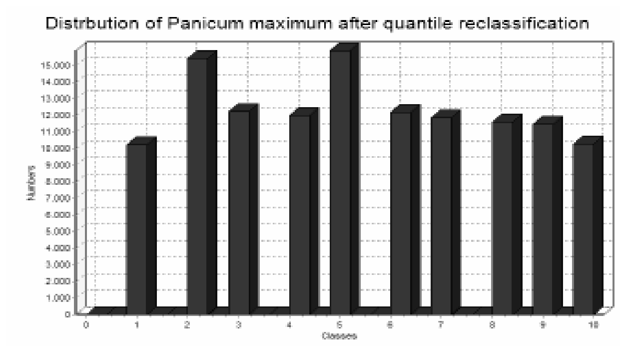

Figure 3: Distribution of Panicum maximum after the quantile reclassification of the distribution in Figure 3. into 10 classes

The distance harmonic mean algorithm was developed to determine home ranges from intensity of activity (Dixon & Chapman, 1980) and gives a high weight to every single observation and is therefore suitable for datasets with a small sample size. The algorithm is suitable for parametric and non-parametric species distribution, but has an average generalization power (Hirzel & Arlettaz, 2003).

The latter method proved to be successful for wildebeest sightings in the wet season. The same procedure was also applied to the wildebeest sightings in the dry season and to the zebra sightings in the dry and wet season (*Appendix 6*). For all the HS models 5 or 6 factors were retained so a minimum of 80 % variance was accounted for. For the wildebeest and zebra in the wet season reliable HS models were obtained (Boyce index = 1.0, P < 0,05), but in the dry season the models weren't reliable (Boyce index is far from significant, P > 0,3). A possible explanation for this is that it is the result of the smaller sample size of the wildebeest and zebra sightings in the dry season (For wildebeest 296 in the wet and 116 in the dry season. For zebra 432 in the wet and 176 in the dry season). To test this hypothesis the wet season datasets for zebra and wildebeest were split up into smaller datasets for the months February through April 2006 (the period in which the grass species data was collected), which resulted in a wet season dataset of 94 samples for zebra and 88 for wildebeest. The cross-validation of the HS models for these datasets proved to be fairly reliable (Zebra: Boyce index = 0,95, P = 0,09. Wildebeest: Boyce index = 0,81, P

= 0,13) (*Appendix 7*). This suggests that it is unlikely that sample size is the cause of the bad quality of the HS model in the dry season.

The overall marginality of the wildebeest in the wet season is 0,58 and of the zebra 0,37 (*Appendix 6*), indicating that the average wildebeest resource preference differs more from the average available resources than that of zebra. There is hardly any difference between the specialization of wildebeest (1,096) and zebra (1,039), indicating that wildebeest and zebra are not very sensitive to variations from their optimal habitat type.

The first derived factor calculated by the ENFA explains 100% of the marginality (by default) (Hirzel *et al*. 2002). This indicates that both species select areas with high *U. mossambicensis* abundance and have a slight preference for areas with a higher HBM (*Appendix 6*). Furthermore zebra avoid areas with high species richness and high abundances of *C. plurinodes* and *B. deflexa* in the wet season. Wildebeest tend to avoid areas with high abundances of B*. deflexa*, *P. maximum*, *E. cenchroides* and *E. scoparius*. The other factors show the sensitivity of the species to changes in the optimal values of the GQQPs. Only the absolute values are of interest here (Hirzel *et al*. 2002). In the wet season zebras are sensitive to a decrease in the abundance of *U. mossambicensis* (second factor) and increases in the abundance of *E. cenchroides* and *E. scoparius* (third factor). Wildebeest are sensitive to increases of *D. eriantha*, *P. maximum* (second factor) and *E. cenchroides* and *E. scoparius* (third factor). Both species are sensitive to increases in the SR (fourth factor).

The resource maps computed from the ENFA with the harmonic mean variable show a rather patchy distribution of the suitable habitat throughout the GMPGR (*Appendix 8*). However, some areas can be marked out as areas of high habitat suitability. This map supports the general idea that there are less highly suitable resource areas for wildebeest than there are for zebra in the GMPGR, which was also suggested from the marginality factors.

DISCUSSION

Random-stratified sampling

Random-stratified sampling proved to be a suitable technique. With many predictor variables the twice-standard-error curves diverge nearing one or both ends of the range of values on the X-axis (*Appendix 5*). A subdivision of the environmental factors (*Table 1*) into more classes would possibly give a better spread of the sample locations over the whole range of values, giving a more accurate estimate of the course of the response curve.

Herbaceous biomass measurement

The herbaceous biomass was measured with a disk pasture meter, which proved to be a useful instrument that is convenient to use in combination with the step-point sampling method. In this study the disk pasture meter was calibrated using fresh weight. Many studies use dry weight to measure the biomass (e.g. Dörgeloh, 2002; Harmoney *et al*. 1997; Rayburn & Lozier, 2003; Sanderson *et al*. 2001). However, the disk pasture meter calibration performed in this study with fresh weight, produced similar results to a study by Dörgeloh (2002) in a comparable area in South Africa with dry weight. The fit of the trendline in a scatterplot of the disk height and the biomass is the same (This study: R^2 = 0,651; Durgeloh: R^2 = 0,647) and the conversion from disk height (cm) to biomass (kg*Ha) is also comparable (This study: HBM = 263,5*height; Durgeloh: Above ground standing biomass = 681,9 + 300,4*height). Therefore, it is unlikely that the use of fresh weight in this study causes irregularities. Further experiments need to be conducted to compare fresh weight and dry weight disk calibrations.

Grass quality and quantity parameter predictions

The accuracy of GQQP predictions wasn't very high. Especially the cross-validation of the models usually pointed out a low model stability (*Table 4*). This lack of accuracy can be caused by the acquisition date of one of the predictor variables; the Landsat ETM+ image (21st May 2001). The acquisition date is in the late wet season (roughly a month after the data collection for this study took place) and 5 years prior to this study. In that period the vegetation in the GMPGR could have changed. Introducing a soil type or soil texture map as predictor variable could enhance the model quality (Mutanga *et al*. 2004). Accurate soil maps are scarcely available, especially at the spatial scale of the GMPGR. Perhaps including more indexes derived from Landsat images or DEMs, could give better insight into the spatial patterns of soil characteristics and soil wetness (Franklin, 1995; Johnson, 1969; Peterson, 2005). These indexes are on the other hand mainly used for data compression (less layers are needed) and comparison of different images (Crist & Cicone, 1984).

The GAM method proved to be a flexible and empirical method for predicting the GQQPs. Arguably, GAM response curves of the predictor variables and response variables don't give as much interpretable information as parametric models would do. Because the GQQP predictions were used to predict grazer HS, the importance of model fit was outweighed by the importance of model interpretability, which is why the empirically based GAM is favored. The drawback to this is that because some interpretability is sacrificed, decisions based on the response curves are not facilitated by GAM models.

Using the different bands of multispectral satellite images and NDVI as predictor variables in the GAM, further hinders the interpretability of the response curves. Some Landsat bands and the NDVI have been correlated to several geological, ecological or environmental variables. For instance, NDVI has been correlated to percentage grass cover (Liu *et al*., 2004), species richness (Gould, 2000), biomass (Schino *et al.* (2003), leaf area index (Carlson & Ripley, 1997) and crown closure (Xu *et al.* 2003). When looking at the response curve of *U. mossambicensis* to NDVI (*Appendix 5*), it can not be retrieved which of the above variables influences the abundance of *U. mossambicensis.*

Resource maps

ENFA proved to be a useful method in this study, mainly because it works with presence data only and calculates ecologically meaningful factors, but it has limitations. For this study the main limitation is that the results obtained from the ENFA are applicable to this study area and caution should be made when applying the results universally. In this study the marginality of wildebeest was higher than that of zebra, which could imply that the available habitat in the GMPGR is more suitable for zebra than for wildebeest. It could also imply that zebra are more flexible in their diet choice and adapt better than wildebeest to the available habitat. ENFA doesn’t calculate the fundamental niche, but only the realization of the niche in the study area (Hirzel et al. 2002).

The quantile reclassification of the GQQPs, as applied in this study, is not a common technique in other studies. More research needs to be done on the use of quantile reclassification to explore the advantages and disadvantages this technique brings along.

The algorithm used to calculate the resource maps from the factors computed by the ENFA is the distance harmonic mean algorithm. This algorithm calculates HS by the density of the sighting location points in the environmental space (Hirzel, 2004). When using sighting density to extract HS, the assumption is made that an increased number of sightings in an area is due to ecological or behavioral processes and not due to an increase in observation frequency in that area (Hirzel & Arlettaz, 2003). In this study increased sighting density in certain areas could have been the result of a higher occurrence of the observed grazer species in that area, and thus presumably a higher HS. However, it is also likely that increased sighting density is the result of a higher visiting frequency to certain areas. Although the observations are done by volunteers that drive through the whole area, it is likely that certain areas are visited more frequent than others. The median algorithm is the only algorithm available in Biomapper that doesn’t make use of sighting density to calculate HS. It makes use of the species distribution in the ecological niche factor space and assumes that the best habitat is the median species distribution on every factor (Hirzel, 2004). However, this algorithm didn't produce reliable results (Boyce index = 0,25, P = 0,09) for the test dataset (Wildebeest sightings in the wet season).

It proved possible to predict grazer habitat suitability and thus grazer distribution patterns through the distribution of the eight most dominant grass species (average abundance > 4%), the herbaceous biomass and the species richness. It's not surprising that comparable results were found for zebra and wildebeest, because their geographic range and habitat selection is similar (Hirst, 1975). Notable was that the only GQQP positively influencing habitat suitability to a big extent for zebra and wildebeest was the *U. mossambicensis* abundance. Taylor & Walker (1978) found that *U. mossambicensis* formed 26 % of the diet of large herbivores. Only *Digitaria pentzii,* (hardly present in the GMPGR (ARC, 2004)), which was far more abundant, formed a larger part of the diet.

Panicum maximum is a grass species that has a high grazing value (Oudtshoorn,1999), but high abundance of *P. maximum* is avoided by zebra and wildebeest (*Appendix 6*). This negative correlation is probably not caused by the grass itself, but by the environment the grass grows in. *P. maximum* grows in shade and damp, fertile soils, along riverbeds and under trees (Oudtshoorn,1999). Zebra and wildebeest have a preference for open areas (Hirst, 1975). This is probably the reason *P. maximum* is avoided by zebra and wildebeest. The same counts for *B. deflexa* which is an average grazing grass and grows in the shade (Oudtshoorn,1999). The density of the vegetation could thus be a more important factor influencing herbivore distribution than the grazing value of the grass species. Incorporating variables like tree density and area openness in the ENFA, could give a decisive answer about this.

That a reliable HS model could be fitted in the wet season and not in the dry season, can be explained by the fact that zebra and wildebeest select a smaller range of grass species in the wet season and are forced to expand their diet in the dry season (Ben-Shahar, 1991). Because the grazers eat practically all grass available in the dry season, their distribution can not be explained by their food selection, but is more determined by other factors (e.g. water availability and shelter). Another explanation for this difference lies in the sampling method of the grazer sighting locations. The locations are recorded by volunteers that drive or walk around through the GMPGR, recording every grazer that can be observed from the vehicle or their position in the field. In the wet season the vegetation is dense and a relatively high percentage of the observations are done in the open areas (where *U. mossambicensis* grows). This would mean that a more accurate distribution of the grazers is obtained from the sightings in the dry season, which means that the grazer distribution can not accurately be predicted by grass species distribution. A third explanation can be that the GQQPs that influence the grazer distribution in the wet season also influence the grazer distribution in the dry season, but that the values of the GQQPs differ in the dry season. The GQQP maps have been created with wet season data. Due to grazing or other environmental factors the GQQP values might have changed in the dry season.

Ben-Shahar & Coe (1992) discus that it is more likely that wildebeest and zebra select certain grass communities containing highly nutritious species in a certain season, than focusing on a certain grass species. This study suggests that a high abundance of one certain grass species mainly determines the diet of wildebeest and zebra in the wet season and that they avoid areas of relative high grass species richness. Hirst (1975) concludes that wildebeest have a preference for areas of short grass. This study shows that wildebeest have a slight preference for an above average herbaceous biomass. Presuming short grass has a low biomass, this means wildebeest prefer relatively high grass in the wet season.

Hardly any studies have focused on habitat suitability mapping by relating continuous resource variables to animal distribution, as is done in this study. Most studies either focus on assessing habitat suitability by relating discrete landcover classes to animal distribution or continuous remotely sensed variables (e.g. NDVI) to animal distribution (Leyequien *et al.*, In press). Heitkönig *et al.*

(2003) used canonical discriminant functions to classify wildlife species occurrence in the Okavango Delta directly from Landsat TM (wet season) and ETM+ images (dry season). In the wet season it proved possible to get fairly accurate classifications of occurrence for certain animal species. In the dry season the results were less successful. Animal distribution is predicted by relating animal sighting locations to digital numbers of satellite images. The advantage of the method described in our study is that more information about the animal food preference is generated. However, both studies aren't successful in predicting animal distribution in the dry season.

This study describes a method that is suited to obtain grazer resource preference in a specific area, but is less suited for studying the preferred food resources of a certain grazer universally. For wildlife and range management this method provides detailed information on the food selection of grazers within a certain area. The method simultaneously gives insight into grazer food preference and the spatial distribution of the preferred food resources in the area. Further research needs to be done to explore the full potential of this method. Especially the legitimacy of quantile reclassification of predictor variables needs to be examined. The main uncertainty in this study is probably the questionable quality of the grazer sighting locations. A bigger sample size to measure the GQQPs and a random-stratified sampling technique with more strata (more subclasses of environmental predictors), would probably enhance the accuracy of the GQQP maps.

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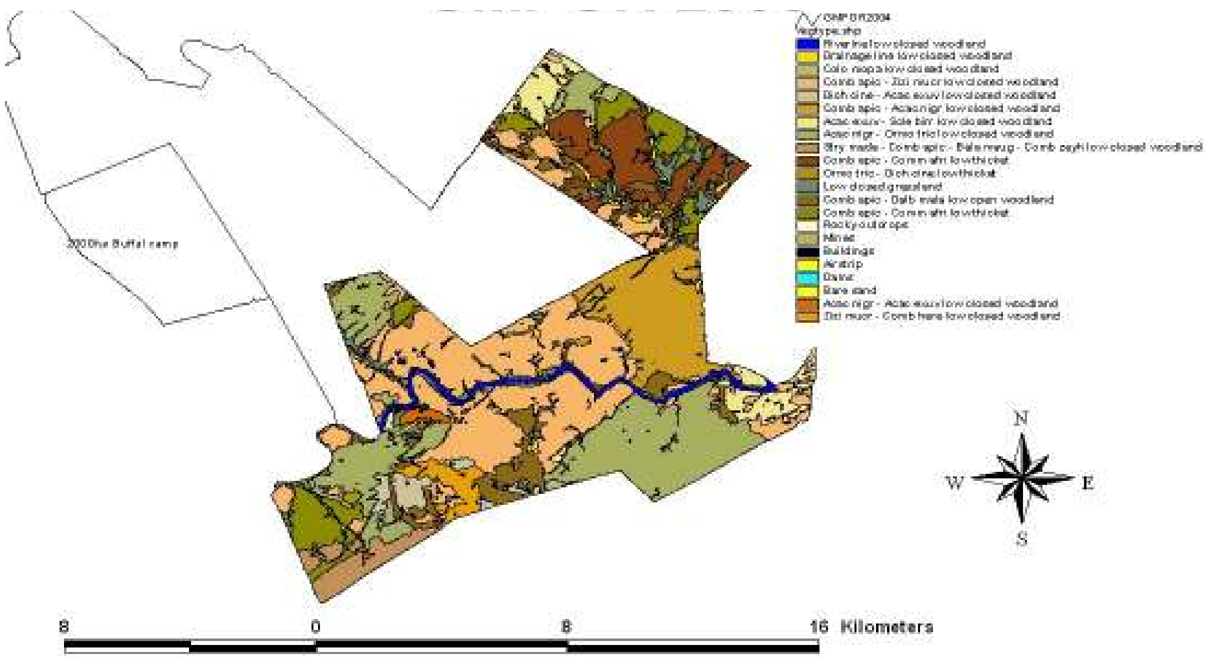
APPENDIX 1: Forest type classification map

Forest type classification map of a part of the Greater Makalali Private Game Reserve (GMPGR) (Druce, 2000)



APPENDIX 2: Accuracy Step Point Sampling

Comparison of the sampling areas that were sampled twice, walking a different route, to estimate the accuracy of this sampling method. The comparison were done making use of the similarity ratio of Sörensen. The locations sampled twice (top) had an average similarity of 79 %. The randomly paired locations (bottom) had a similarity of 44 %.

Similarity double sampled and random paired plots

Double sampled plots

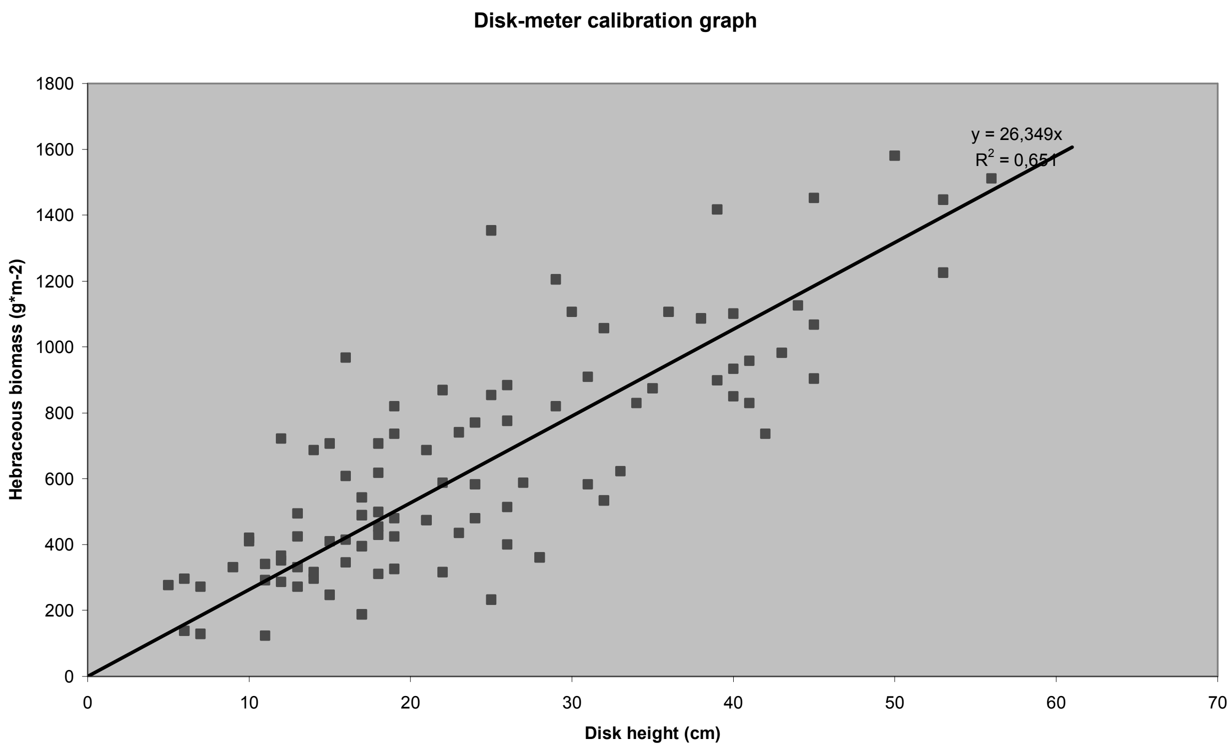
Pairs	ARISTIDA	UROMOSAM	Bare Soil	DIGERIAN	ERARIGID	ENNEAPOG	Forbs	BRADEFLE	PANMAXIM	POGSQUAR	CYMPLURI	MELREPEN	Other grass	THETRIAN	BOTRADIC	HETCONTO	SCHPAPPO	Similarity
1	0	73	13	1	1	0	2	0	8	0	0	0	0	0	0	0	2	
	0	77	5	0	0	0	6	0	11	0	0	0	1	0	0	0	0	88%
2	1	0	10	32	0	12	8	13	13	0	5	1	4	0	0	1	0	
	3	0	5	27	0	28	8	7	8	0	8	2	3	0	1	0	0	77%
3	1	0	15	4	0	12	25	22	1	0	2	5	10	0	0	3	0	
	1	0	7	0	0	18	32	20	4	0	3	4	6	0	1	2	2	80%
4	12	0	9	14	0	5	23	2	6	0	2	5	14	0	6	2	0	
	11	0	4	5	0	10	26	2	13	0	2	5	11	0	4	6	1	80%
5	0	4	6	22	0	8	16	11	4	0	4	7	5	0	10	3	0	
	4	0	10	28	4	11	7	6	4	0	12	1	1	0	6	6	0	68%
6	4	0	12	0	0	22	24	16	4	0	6	4	6	0	0	2	0	
	15	0	18	1	0	19	12	6	2	0	7	13	2	0	2	3	0	69%
7	2	34	4	18	1	0	8	2	11	0	0	0	10	0	0	0	10	
	0	36	4	15	4	0	13		3	0	0	0	9	0	3	0	13	86%
8	0	0	5	26	0	16	17	7	5	0	9	0	12	0	0	2	1	
	6	1	10	23	0	15	9	5	2	0	13	1	10	1	0	4	0	80%
																	Average:	**79%**

Random paired plots

Pairs	ARISTIDA	UROMOSAM	Bare Soil	DIGERIAN	ERARIGID	ENNEAPOG	Forbs	BRADEFLE	PANMAXIM	POGSQUAR	CYMPLURI	MELREPEN	Other grass	THETRIAN	BOTRADIC	HETCONTO	SCHPAPPO	Similarity
1	2	34	4	18	1	0	8	2	11	0	0	0	10	0	0	0	10	
	1	16	10	10	0	3	16	3	22	0	1	1	9	4	0	4	0	61%
2	1	68	0	0	0	0	19	4	1	0	0	0	2	0	0	0	5	
	0	88	2	0	0	0	10	0	0	0	0	0	0	0	0	0	0	78%
3	0	18	3	21	0	0	17	12	5	0	3	1	5	0	8	0	7	
	7	2	14	27	3	12	18	3	1	0	2	0	3	0	1	4	3	56%
4	3	3	9	16	3	1	15	3	5	0	13	1	15	1	0	8	4	
	13	3	6	7	2	18	24	11	2	1	0	4	5	0	3	0	1	49%
5	3	0	5	27	0	28	8	7	8	0	8	2	3	0	1	0	0	
	0	60	7	12	5	0	5	0	5	0	0	0	0	1	0	0	5	27%
6	3	47	5	0	0	0	32	0	3	0	0	0	0	1	9	0	0	
	11	0	12	1	0	16	16	22	1	0	3	0	7	1	9	1	0	35%
7	0	56	5	5	0	0	3	0	5	0	1	0	0	0	24	0	1	
	0	4	6	22	0	8	16	11	4	0	4	7	5	0	10	3	0	32%
8	0	71	6	0	0	0	20	3	0	0	0	0	0	0	0	0	0	
	13	1	5	8	0	9	10	0	1	0	0	5	1	0	34	6	7	16%
																	Average:	**44%**

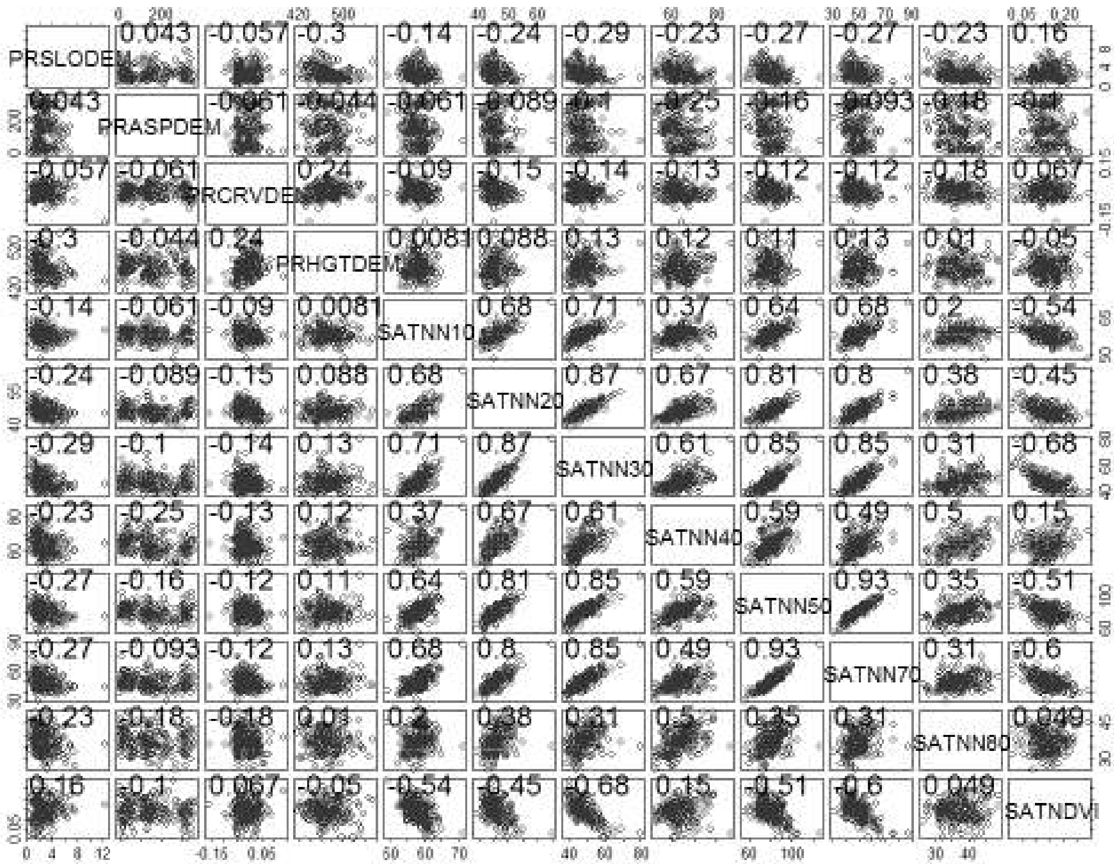
APPENDIX 3: Disk Pasture Meter calibration

Graph of the disk height and the herbaceous biomass (g*m^{-2}). A linear and a log-transformed trendline are fitted into the scatterplot. The linear trendline has the best fit (R^2 = 0,651). (log linear transformation: R^2 = 0,601; square root transformation: R^2 = 0,650)



APPENDIX 4: Correlation predictor variables

Correlation coefficients between the predictor variables. Variables with a correlation higher than 0,85 will not be used in the GAM as predictor variables. Therefore SATNN30 (Landsat band 3) and SATNN70 (Landsat band 7) are excluded from the model calculation.



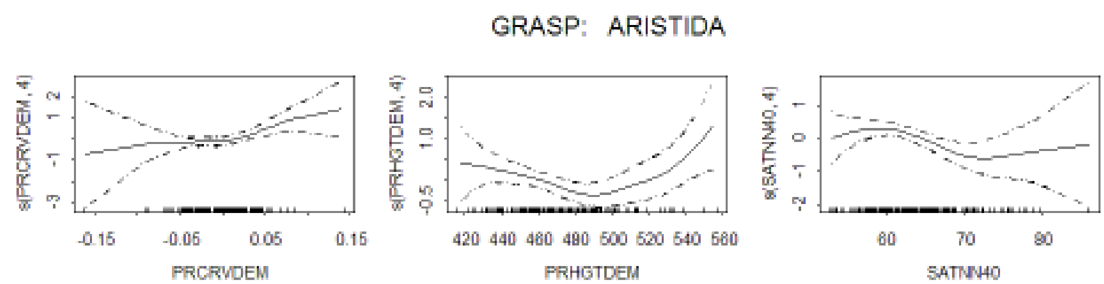
APPENDIX 5: Response curves predictor variables

Significant ($p < 0,05$) response curves of the predictor variables and the GQQPs, derived from the GAMs. The continuous line represents the predicted model. The dashed lines represent upper and lower twice-standard-error curves. The response curves for HC and the grass species with an average abundance lower than 4% are not included, since their GQQPs are not used in further analysis (see chapter 'Results: Grass quality and quantity parameter predictions'). The response curves were produced in GRASP (Lehman *et al*., 2002). The table on the right shows the used predictor variables and their reference code as used in GRASP.

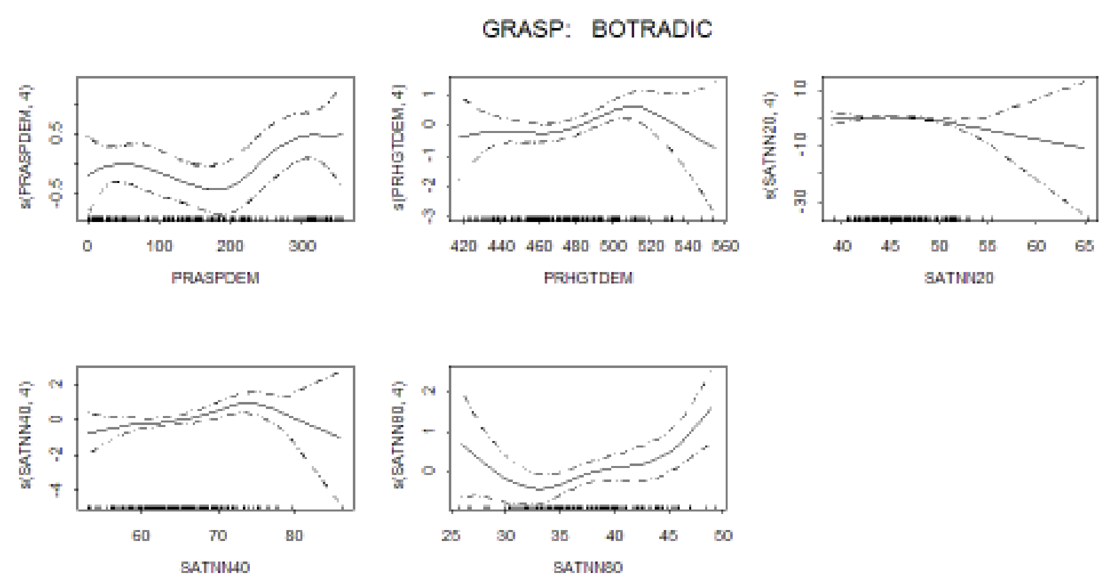
GAM predictor variables

Variable	Code
Slope	PRSLODEM
Aspect	PRASPDEM
Curvature	PRCRVDEM
Altitude	PRHGTDEM
Landsat band 1	SATNN10
Landsat band 2	SATNN20
Landsat band 3	SATNN30
Landsat band 4	SATNN40
Landsat band 5	SATNN50
Landsat band 7	SATNN70
Landsat band 8	SATNN80
NDVI	SATNDVI

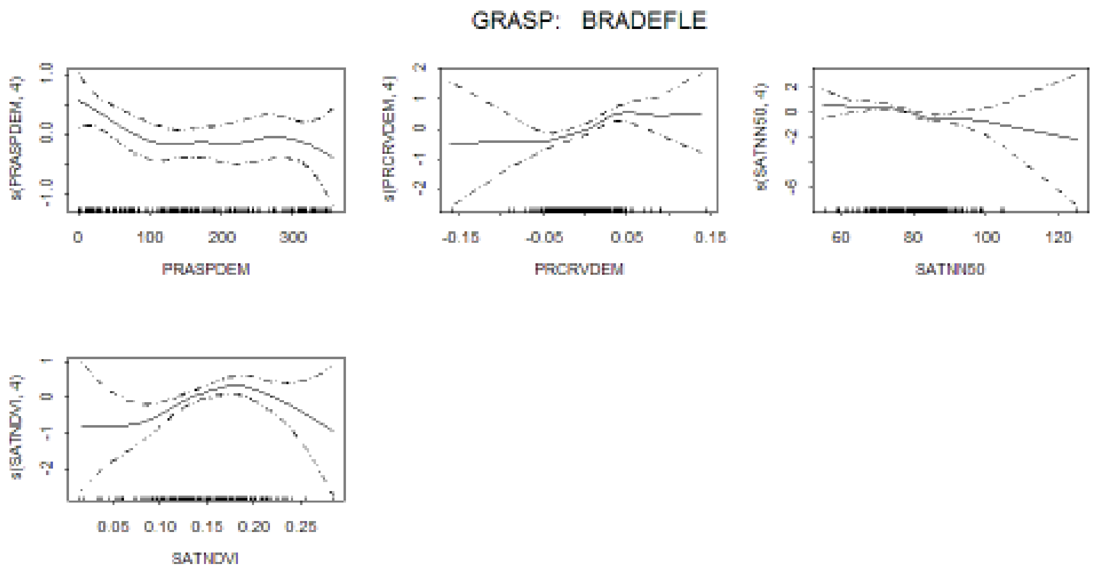
Response curves *Aristida* species:



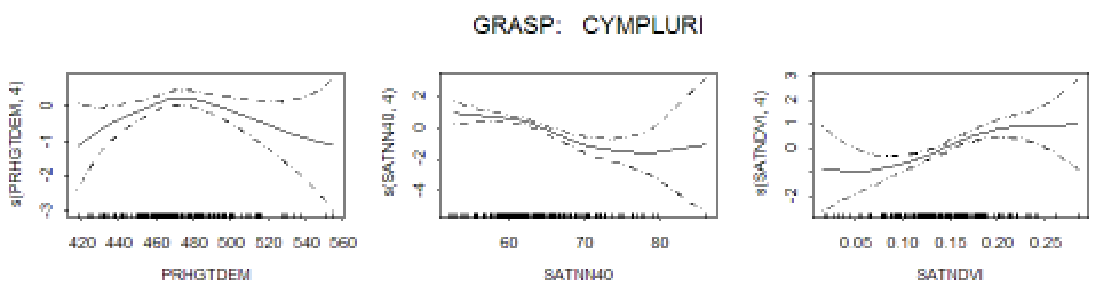
Response curves *B. radicans*:



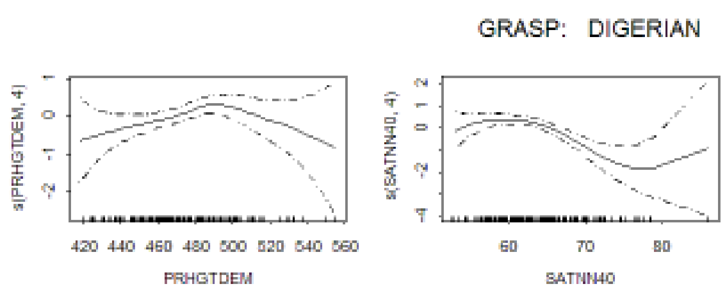
Response curves *B. deflexa*:



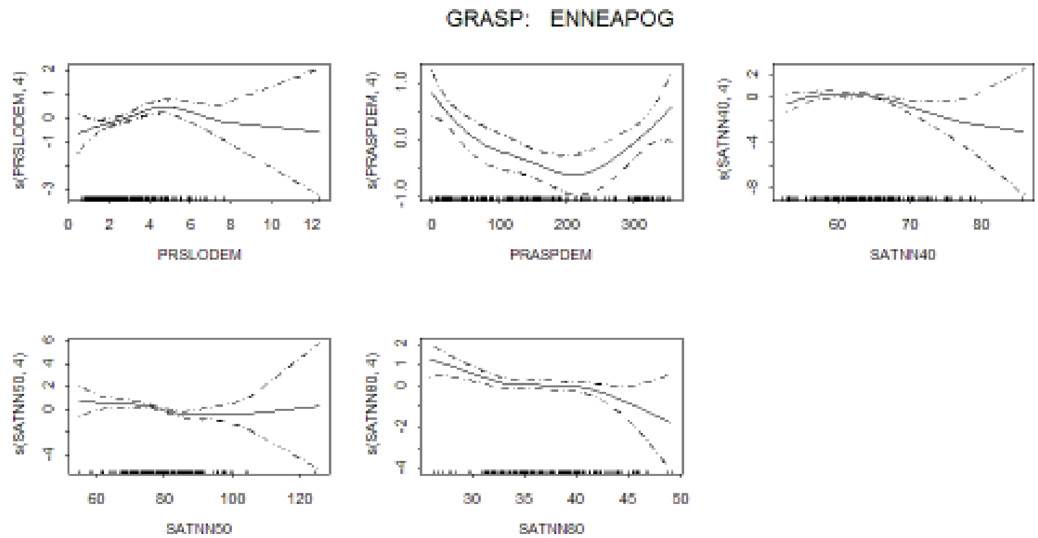
Response curves *C. plurinodes*:



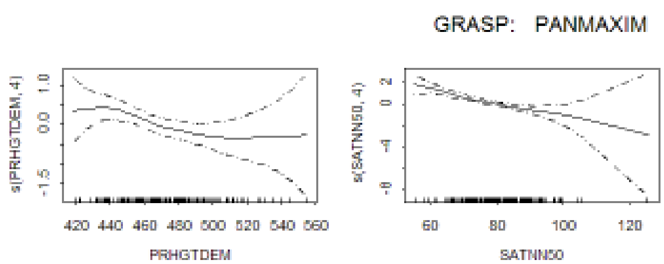
Response curves *D. eriantha*:



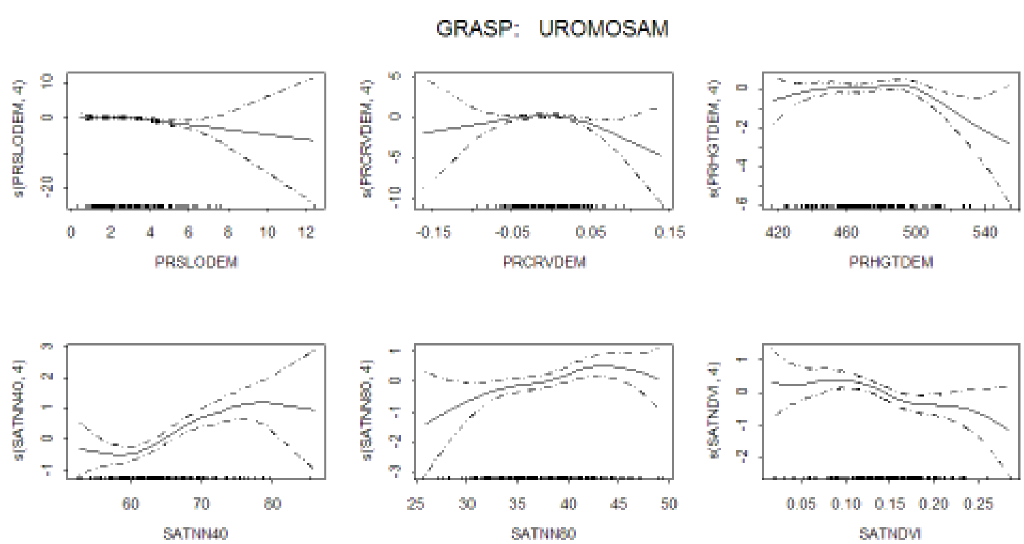
Response curves *Enneapogon* species:



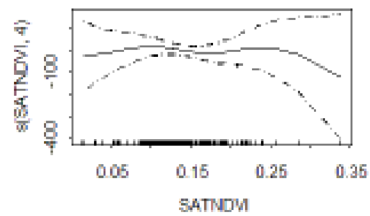
Response curves *P. maximum*:



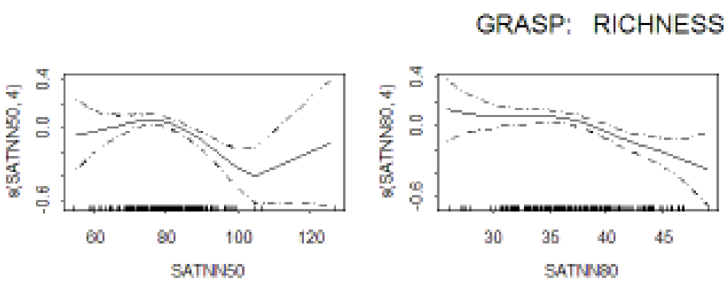
Response curves *U. mossambicensis*:



Response curve herbaceous biomass ($g*m^{-2}$):



Response curve grass species richness:



APPENDIX 6: Results ENFA

Results of the ENFA, when the GQQPs are uniformly distributed and the distance harmonic mean algorithm is used in Biomapper 3.2 (Hirzel *et al*. 2006). Only the factors used to calculate the HS model (at least 80 % of the variance explained) are shown in this table.

Zebra wet season

Score matrix	81 % variance explained				
Factor	1	2	3	4	5
U. mossambicensis	**0,467**	**0,716**	-0,308	-0,246	0,396
Herbaceous biomass	**0,101**	0,093	0,118	0,287	0,213
Aristida sp.	-0,013	-0,275	-0,153	-0,233	-0,081
D. eriantha	-0,117	0,341	0,362	-0,048	-0,232
B. radicans	-0,213	-0,103	-0,373	0,021	0,077
Enneapogon sp.	-0,233	0,285	**-0,512**	0,575	0,071
P. maximum	-0,248	0,359	0,368	0,001	-0,179
C. plurinodes	**-0,423**	0,162	-0,318	0,197	-0,314
Grass species richness	**-0,439**	0,195	-0,145	**-0,656**	0,032
B. deflexa	**-0,474**	0,043	0,28	-0,024	**0,771**
Marginality:	0,37				
Specialisation:	1,039				
Boyce index:	1 +- 0				

Wildebeest wet season

Score matrix	81 % variance explained				
Factor	1	2	3	4	5
U. mossambicensis	**0,425**	0,259	-0,442	0,508	**-0,621**
Herbaceous biomass	**0,021**	0,079	-0,041	-0,174	-0,219
B. radicans	-0,059	-0,371	-0,042	-0,029	0,115
D. eriantha	-0,115	**0,435**	-0,199	-0,36	0,264
Aristida sp.	-0,288	-0,137	0,414	0,418	-0,417
C. plurinodes	-0,325	-0,32	-0,243	-0,029	-0,076
Grass species richness	-0,339	0,062	-0,244	**0,578**	0,15
B. deflexa	**-0,393**	0,409	0,309	0,103	-0,057
P. maximum	**-0,4**	**0,454**	0,05	-0,245	0,084
Enneapogon sp.	**-0,429**	-0,318	**-0,611**	0,014	-0,52
Marginality:	0,58				
Specialisation:	1,096				
Boyce index:	1 +- 0				

Zebra dry season

Score matrix	85 % variance explained					
Factor	1	2	3	4	5	6
U. mossambicensis	0,244	0,444	-0,013	0,609	0,274	-0,227
D. eriantha	0,209	0,236	0,046	0,36	-0,03	0,456
Enneapogon sp.	0,141	-0,521	0,035	0,124	0,27	-0,122
Aristida sp.	0,08	0,274	0,317	0,024	-0,249	-0,402
Herbaceous biomass	-0,01	-0,081	0,563	0,178	0,418	0,17
C. plurinodes	-0,226	-0,065	-0,387	0,315	-0,576	-0,409
B. radicans	-0,231	-0,249	-0,464	-0,033	0,062	-0,144
Grass species richness	-0,355	0,56	0,174	-0,419	0,162	0,03
P. maximum	-0,439	-0,11	-0,202	0,14	-0,305	0,551
B. deflexa	-0,669	0,044	0,378	0,396	0,399	-0,206
Marginality:	0,24					
Specialisation:	1,062					
Boyce index:	0,5 +- 0,33					

Wildebeest dry season

Score matrix	81 % variance explained				
Factor	1	2	3	4	5
U. mossambicensis	0,346	-0,162	0,137	-0,266	0,063
D. eriantha	0,041	-0,576	0,209	0,045	-0,316
B. radicans	0,03	-0,015	-0,392	0,018	0,155
Aristida sp.	-0,067	0,203	0,013	-0,17	-0,091
Herbaceous biomass	-0,095	0,016	0,276	0,202	0,407
Enneapogon sp.	-0,264	0,55	0,193	0,285	-0,209
Grass species richness	-0,322	0,063	0,177	-0,276	0,693
B. deflexa	-0,433	-0,402	-0,21	0,633	0,046
C. plurinodes	-0,499	0,158	0,549	-0,203	0,004
P. maximum	-0,504	-0,327	-0,542	-0,508	-0,415
Marginality:	0,443				
Specialisation:	1,049				
Boyce index:	0,6 +- 0,58				

APPENDIX 7: Results ENFA II

Results of the ENFA, when the GQQPs are uniformly distributed and the distance harmonic mean algorithm is used in Biomapper 3.2 (Hirzel *et al*. 2006). Only the grazer sighting locations of February, March and April 2006 were used in this analysis.

Zebra wet Feb, Mar, Apr 2006

Score matrix	81% variance explained			
Factors	1	2	3	4
U. mossambicensis	**0,443**	-0,378	0,544	-0,407
Herbaceous biomass	0,047	0,385	0,081	0,396
B. radicans	-0,029	-0,413	-0,136	0,075
Aristida sp.	-0,121	0,199	-0,099	-0,418
D. eriantha	-0,211	-0,135	0,314	0,166
P. maximum	-0,236	-0,216	**0,678**	-0,169
Grass species richness	-0,332	-0,277	-0,107	**-0,465**
Enneapogon sp.	-0,336	-0,404	-0,154	0,389
B. deflexa	**-0,415**	**0,436**	-0,056	-0,266
C. plurinodes	**-0,538**	-0,064	0,269	0,048
Marginality:	0,57			
Specialisation:	1,188			
Boyce index:	0,95 +- 0,0866			

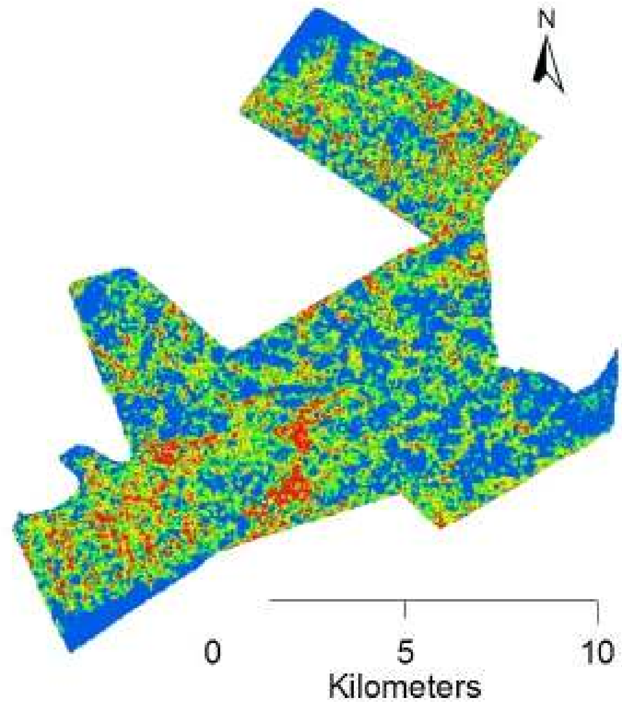
Wildebeest wet Feb, Mar, Apr 2006

Score matrix	85% variance explained				
Factors	1	2	3	4	5
U. mossambicensis	**0,424**	-0,286	0,261	-0,459	-0,278
Herbaceous biomass	-0,03	-0,245	-0,032	0,221	0,011
B. radicans	-0,099	0,372	0,312	0,048	0,076
D. eriantha	-0,229	-0,447	-0,106	0,083	0,555
B. deflexa	-0,278	-0,023	**-0,613**	0,253	-0,17
Aristida sp.	-0,323	**0,539**	0,308	**-0,581**	-0,172
P. maximum	-0,334	-0,202	-0,282	-0,39	**0,548**
C. plurinodes	-0,337	0,103	0,488	0,002	-0,293
Grass species richness	**-0,399**	-0,42	0,082	-0,285	-0,333
Enneapogon sp.	**-0,436**	-0,037	0,167	0,311	-0,232
Marginality:	0,764				
Specialisation:	1,226				
Boyce index:	0,808 +- 0,1302				

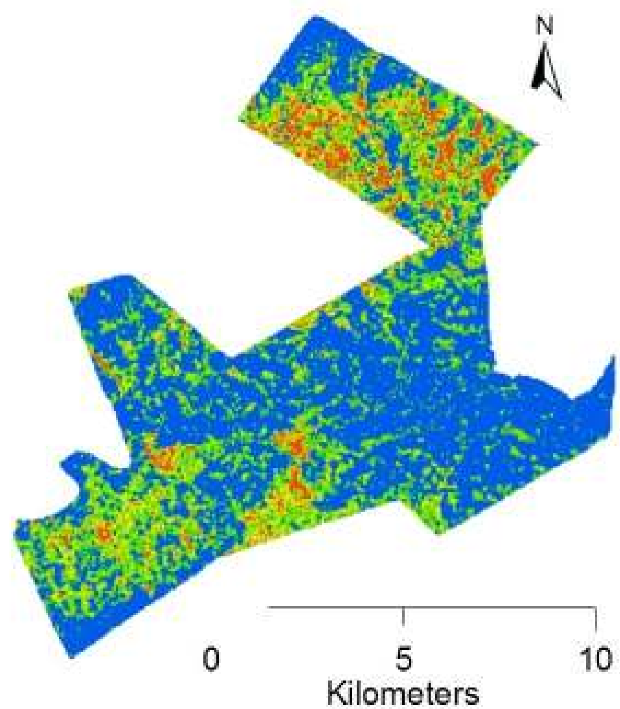
APPENDIX 8: Resource maps

Resource maps for zebra and wildebeest in the wet season in the GMPGR. The maps have a spatial resolution of 30m.

Zebra wet season resource map of the GMPGR



Wildebeest wet season resource map of the GMPGR



Legend

= Low habitat suitability

= Medium low habitat suitability

= Medium high habitat suitability

= High habitat suitability