Beyond the here and now
Herbivore ecology in a spatial-temporal context
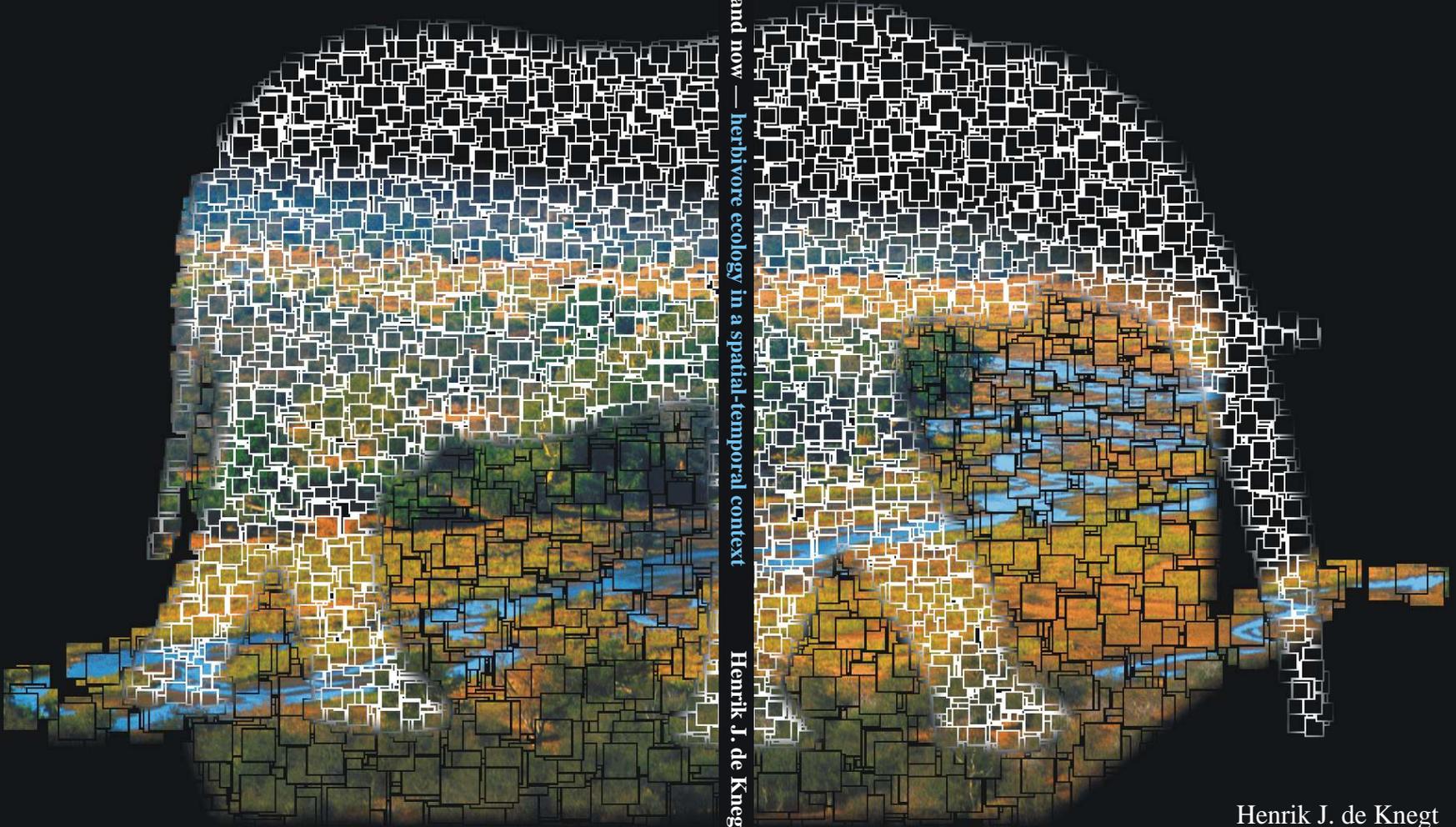
Henrik J. de Knegt

Beyond the here and now

Herbivore ecology in a spatial-temporal context

Beyond the here and now

Herbivore ecology in a spatial-temporal context

Henrik J. de Knegt

To my parents

Contents

1

General introduction

*E*cology studies the interactions that determine the distribution and abundance of different types of organisms (Begon *et al.* 1996; Krebs 2008). These distributions are rarely uniform and continuous in space and time, and the identification of the physical, chemical and biological features and interactions that determine these distributions is a fundamental question in ecology (Begon *et al.* 1996; Mackey & Lindenmayer 2001; Elith & Leathwick 2009). Thus, the primary variable of interest is the spatial-temporal density (or presence/absence) of organsms (that is, the number of organisms located within a unit of area or volume at certain spatial coordinates at a certain point in time), and the way organisms are affected by, and how they affect, their biotic and abiotic environment is one of the cornerstones of ecological research (Turchin 1998; Currie 2007; Elith & Leathwick 2009).

All organisms in nature are where we find them because they have moved there (Begon *et al.* 1996). This is the case for even the most apparently sedentary of organisms, such as oysters and trees: organismal movement ranges from the passive transport of seeds to the active movements by mobile animals. As a primary mechanism coupling species to their environment, movement of individual organisms is a fundamental characteristic of life (Turchin 1998; Bergman *et al.* 2000; Nathan 2008). It plays a major role in determining the fate of individuals, and ultimately, the dynamics and spatial structure of populations is derived from individual behaviour (Turchin 1991; Nathan 2008).

Species-environment relationships

One of the challenges to understanding the movement and distribution of organisms is understanding the influence environmental heterogeneity exerts on organisms (Morales & Ellner 2002; Romero *et al.* 2009). Environmental heterogeneity creates a non-uniform, spatially and temporally varying distribution of resources and stressors that influence species and species interactions (Addicott *et al.* 1987). The movement strategy that or-

ganisms use while foraging on spatially dispersed resources is crucial to their success in exploiting them (Bell 1991; Viswanathan *et al.* 1999; Zollner & Lima 1999; Bartumeus *et al.* 2005). Moreover, movement by organisms influences the set of prevailing environmental conditions that impinge upon them (Mackey & Lindenmayer 2001). Thus, the way organisms respond to environmental heterogeneity is of major importance for understanding ecological phenomena.

Besides responding to environmental heterogeneity, organisms actively modify their environment and influence that of other species (Erwin 2008). They have been doing so since the origin of life, creating heterogeneity even in the absence of underlying spatial environmental heterogeneity, or modifying the heterogeneity already present (Turner *et al.* 2001; White & Brown 2005; Erwin 2008). For example, interactions among organisms, such as competition and predation, may lead to spatial structuring even in a completely homogenous space (Turner *et al.* 2001). In general, large mammals are thought to be an important mechanism in the creation, modulation and maintenance of environmental heterogeneity (Turner *et al.* 2001). When studying species-environment relationships, the influence of environmental heterogeneity on organisms, as well their influence on environmental patterning thus needs to be considered.

Beyond the here and now

The way organisms relate to their environment has for a long time been analysed spatially and temporarally inexplicit. However, an increasing emphasis has been placed on spatial processes in ecological systems over the past couple of decades, as ecologists begun to appreciate more fully the potential effects of the landscape surrounding a site on organisms at the site (Tilman & Kareiva 1997; Rietkerk *et al.* 2004; Gutzwiller & Riffel 2007). Moreover, it is increasingly being recognized that present-day ecological phenomena are influenced by past events of processes (Wiens & Donoghue 2004; Wolf *et al.* 2009). In other words, ecologists are increasingly recognizing the importance of processes and factors that are "beyond the here and now", as is the main title of this thesis. Namely, beyond *here* is *there*, and beyond *now* are *past* and *future*.

Using these words, ecologists have increasingly recognized the importance of *there* for understanding ecological phenomena *here*, but also the importance of the *past* in understanding the *present*. In this thesis, I will refer to this as the influence of the "spatial-temporal context" in which ecological processes and phenomena take place. Spatial context relates ecological phenomena at a specific location to characteristics of neighbouring locations, while temporal context relates current ecological phenomena to influences from the past. For example, spatial-temporal context may influence organisms by influencing demographic processes, habitat selection, dispersal and conspecific attraction (Cliff & Ord 1981; Legendre 1993; Wagner & Fortin 2005; Dormann *et al.* 2007).

Having introduced the word "context", it is necessary to discuss the issue of "scale", another issue that is a central topic in this thesis. In order to investigate the influence of processes and patterns beyond the here and now, it is crucial to know where here and now end, and thus where the influence of *beyond here* (i.e., the influence of neighbouring locations) and *beyond now* (i.e., the influence of past patterns and processes) starts. Moreover, it is crucial to know how far beyond the here and now we want (or are able) to go. In this thesis, these two crucial components are referred to as the "grain" (or resolution) and "extent" of the analyses. Extent describes the total area or time period under consideration; grain describes the detail (or resolution) of observations (Turner 1989;

Wiens 1989). In general, extent sets the upper bound for generalizations, whereas grain sets the lower limit for the scale of detectable patterns (Rietkerk *et al.* 2002b; Schooley 2006; Meyer 2007). Throughout this thesis, I will adopt the common usage among ecologists when referring to scale, where "large scale" refers to wide areas or long time frames, whereas "small scale" refers to a small spatial extent or short time frame. Note that this differs from cartographic scale (as in 1:100000 on a map), where large scale means highly detailed observations, generally over small extents.

The issue of scale has featured as a central topic in ecological research over the past years (for reviews, see Turner 1989; Wiens 1989; Levin 1992; Schneider 2001; Dungan *et al.* 2002; Gotway & Young 2002). Issues of scale are present in every facet of ecological research: from scales intrinsic to ecological phenomena; scales of observation and measurement; scales of analysis and modelling; and scales of management and policy (Bierkens *et al.* 2000; Wu *et al.* 2006). When relating species to their environment, it is currently widely acknowledged that each species may perceive its environment differently. Hence, because our perception of a landscape may differ from that of the organisms we study, a challenge is to appropriately characterize the scales that are relevant to the organisms under study, and then to accurately measure their response to environmental heterogeneity at those scales (Wellnitz *et al.* 2001).

Moreover, the processes creating environmental heterogeneity operate over a wide array of spatial and temporal scales; from processes acting at broad spatial-temporal scales, e.g., plate tectonics and climatic patterning; to processes operating at fine spatial-temporal scales, e.g., local water and nutrients transport. Consequently, different patterns of environmental heterogeneity are manifested at different spatial-temporal scales, with different processes being dominant at different scales. For example, as Breshears (2006) writes: "From an airplane, we often look out the window and survey the landscape as we begin our final descent. As we get closer to the ground, our focus changes from an initial broad survey of the topography to an increasingly detailed picture of vegetation patterns." The scale multiplicity and scale dependence of pattern, process, and their relationships are therefore central components when trying to understand ecological phenomena (Levin 1992; Peterson & Parker 1998; Breshears 2006).

Thus, through meaningfully extracting ecological information from patterns in species-environment relationships across spatial and temporal scales, while taking into account the influence of spatial-temporal context, we can increase our understanding of the processes that are at work to create the observed patterning in species distributions. This is a search for knowledge in the pure scientific tradition, however, it is crucial if one aims at predicting what will happen to an organism, a population or a community under a particular set of circumstances (Begon *et al.* 1996). Thus, the challenges involved in making better predictions of species' distributions are both theoretical and applied (Guisan *et al.* 2006; Diez & Pulliam 2007), and have consequences for the successful conservation and management of species or ecosystems.

Focus and thesis outline

In this thesis, I focus on species-environment relationships across a range of spatial-temporal scales and with consideration of the influence of spatial-temporal context. The central question dealt with in the following chapters is how spatial-temporal context influences the relationships between species and their environment, and at what scale(s) this context is important. The focus is on the response of organisms to the spatial context

of a site, which I refer to as "environmental context", i.e., the environmental characteristics of the landscape surrounding a site. Moreover, the influence of temporal context is being studied by analyzing the influence of past use of sites on the current patterns of site visitation. Besides the response of organisms to environmental heterogeneity, the role of organisms in creating and maintaining environmental heterogeneity is also being studied. The following chapters report on theoretical studies with hypothetical organisms, and studies based on field data regarding African elephants (*Loxodonta africana*) in Kruger National Park (KNP), South Africa. Elephants are thought to be major agents of habitat change (e.g. Barnes 1983; Ben Shahar 1993), and as a consequence of the rising number of elephants in many protected areas in southern Africa, the ecosystems that contain elephants are perceived to be coming under increasing threat (Scholes & Mennell 2008). However, although I focus on large mammalian herbivores, with elephants as a model species, I contend that the patterns and processes discussed in this thesis are easily translated to other types of organisms or systems.

In Chapter 2, I investigate the influence of topography on the movement of elephants in KNP. This influence is analyzed at different temporal scales: from patterns within a day to varying over the seasons; and different spatial scales: from fine-scale topographic relief to broad-scaled relief. Chapter 3 then asks the question whether and through which mechanisms herbivores can induce spatial patterning in savanna vegetation. Using simulation modelling, I test the assumptions that herbivore-vegetation feedbacks as well as the influence of environmental context are necessary for herbivores to induce spatial vegetation patterning. In Chapter 4, I analyze the patterns of site fidelity by elephants in KNP by analyzing how visits to specific sites in the landscape are related to visits of those sites in the past. Chapter 5 then highlights the interplay between spatial autocorrelation in the residuals of regression methods when analyzing the spatial distribution of a species, and the spatial scaling of species-environment relationships. Using a hypothetical species in an artificial landscale, this chapter shows the consequences of a scale mismatch on such analyses and the interpretation thereof. Chapter 6 analyzes the broad-scale distribution of elephants in KNP, focusing on the spatial scale at which elephants respond to their main resources, i.e., water and forage. This chapter investigates the influence of the scale used for analysis on the quantification and predictability of habitat selectivity. Chapter 7, finally, synthesises the conclusions that can be drawn from the preceding chapters and puts the issues addressed in a broader context of species-environment relationships.

HJ de Knegt, F van Langevelde, AK Skidmore, R Slotow, S Henley, A Delsink, WF de Boer, SE van Wieren & HHT Prins

2

The seasonal and circadian rhythms of terrain-use by African elephants

Before getting too far into studying the influence of spatial heterogeneity on the movement and distribution of organisms, it is usually necessary to ask: how and why is the landscape heterogeneous? Topography usually has a severe influence on landscape heterogeneity, through influencing broad climatic gradients as well as local gradients in soil moisture and nutrients. In savanna ecosystems with intermediate rainfall, this gives rise to pronounced topo-edaphic vegetation patterns, with relatively open vegetation on sandy soils at the crests of catenas, and more dense vegetation on clay soils containing more nutrients and water in the valleys. Valleys and low-lying parts of the catena therefore have vegetation of higher quality and quantity, remaining green for longer in the dry season, therefore being important for herbivores during the dry season. Furthermore, the more densely vegetated lower parts of the catena may supply shade to heat sensitive animals compared to the more open vegetation on the crest of catenas, so that the vegetation at the lower part of the catena becomes important during times of peak temperature. We therefore set out to test the influence of local topography on the spatial distribution of African elephants in a semi-arid savanna ecosystem by testing the hypotheses that elephants (1) move progressively down slope during seasonal dry periods, and (2) move to lower parts of the catena during times of peak temperature (i.e., midday), going back to higher parts of the catena during cooler periods of the day. The results show that elephants organize their use of topographically-mediated environmental gradients around seasonal and circadian rhythms, in ways that are consistent with known eco-physiological processes. In the dry season, and during midday, the elephants preferred to be predominantly at the lower parts of the catena, while being distributed indifferently over the catenary gradient in the wet season and during the night. We conclude that local topography is important in savanna ecosystems, because it interacts with climate to mediate the distribution of nutrients and moisture over the landscape, thereby influencing the patterning and productivity of vegetation, and ultimately affecting the distribution of large herbivores.

Introduction

Biogeographical analyses often relate the spatial distribution of plant and animal species to topographic indices (e.g., elevation, slope, aspect). For animals, topography may directly affect movements by imposing considerable energetic costs on travel (Wall *et al.* 2006). However, it mostly affects animals indirectly through affecting the flow of energy and matter through a landscape, creating spatial and temporal variation in (1) the resources that organisms require, e.g., mineral nutrients and water, and (2) the environmental conditions that influence the physiology of organisms, e.g., temperature and air/water pressure (Mackey & Lindenmayer 2001; Turner *et al.* 2001; White & Brown 2005; Korner 2007; Hirzel & Le Lay 2008). It has therefore been argued that topography comprehensively characterizes the quality of habitat, replacing a combination of different resource and stress gradients in a simple way (Austin 2002; Legendre *et al.* 2009). Because topographic indices are often easily measured in the field, as well as accurately estimated using airborne sensors, they can be invaluable for understanding species distributions (Austin 2002).

However, the correlations of topography with resource and stress gradients are sensitive to the scale of observation. At large spatial scales, topography influences climatic variables such as temperature, atmospheric pressure, solar radiation and precipitation. Such altitudinal gradients are therefore often important predictors of large-scale variability in species distributions (Stevens 1992; White & Brown 2005). At smaller spatial scales, however, other patterns and processes dominate, and the broad-scale smooth relationships appear increasingly fuzzy at fine spatial scales (White & Brown 2005; Korner 2007). Hence, when considering fine-scale environmental variation, altitude in itself has often little descriptive power, as other factors such as slope and relative terrain position then become important (Korner 2007; Rennó *et al.* 2008).

Fine-scale topographic variation plays an important role in determining water movement (Chamran *et al.* 2002). This topographical influence on water flow is a driving force behind soil differentiation, leading to gradients of increasing soil moisture and nutrient content from the hill top to the valley bottom, thereby having severe consequences for vegetation patterning and ecosystem functioning (Chamran *et al.* 2002; Shorrocks 2007; Hartshorn *et al.* 2009). Hence, fine-scale topography interacts with broad-scale climatic conditions to produce systematic topo-edaphic variability in available soil moisture and nutrients (Scholes & Walker 1993; Venter *et al.* 2003). These topographically mediated gradients are maximized under a semi-arid climate and in areas with gentle slopes, conditions characteristic for most African savanna systems (Venter *et al.* 2003; Hartshorn *et al.* 2009).

The typical topography of such savannas is a series of undulations that, together with the associated soil and vegetation, are known as "catenas" (Bell 1971; Shorrocks 2007). Rain falling on an undulation gravitates from the top, via the slopes, to the bottom, carrying with it soluble material and soil particles so that the top of the catena becomes progressively leached of organic matter and comes to consist of shallow and course sandy soil. In contrast, the lower lying areas come to consist of clay, with high nutrient content and a high capacity for water retention (Bell 1971; Venter *et al.* 2003; Shorrocks 2007). The hill slopes show a gradient between these two extremes. This generally gives rise to gradients from nutrient-poor and open vegetation on the upland crest to nutrient-rich and dense vegetation in the valley (Ben Shahar 1990; Du Toit *et al.* 2003; Venter *et al.* 2003; Asner *et al.* 2009; Hartshorn *et al.* 2009).

The catenary gradients in soil moisture and nutrient availability interact with seasonal rainfall patterns in governing the abundance and quality of vegetation, which has a major influence on the distribution of herbivores (Bell 1971; Nellemann *et al.* 2002; Du Toit 2003). In dry periods, the soil on the higher parts progressively desiccates, while plants growing towards the valley bottom have access to soil moisture for longer periods (Du Toit 2003). This causes herbivores to concentrate their feeding in zones that shift up and down the catenary gradient through the seasonal cycle, moving progressively down slope in the dry season as the availability of moist, green and nutritious feeding declines in the uplands, and moving up the profile again in the wet season (Bell 1971; Pellew 1984; Nellemann *et al.* 2002; Du Toit 2003; Smit *et al.* 2007a).

Moreover, besides seasonal patterns in habitat selection along the catenary gradient, we expect savanna herbivores to select different sites along the catenary gradient at different times of the day. Savannas are generally hot and expose animals to large fluctuations in ambient temperature, ranging from extreme peak temperatures of more than 50°C during midday to below 0°C at night (Kinahan *et al.* 2007a). This poses physiological challenges to thermal homeostasis in endothermic animals during periods of extreme temperatures (Kinahan *et al.* 2007a,b). This especially applies to large animals, such as African elephants (*Loxodonta africana*), that may face physiological problems of dissipating heat during spells of extremely high ambient temperatures (Kinahan *et al.* 2007a). Since canopy cover generally increases when going down the catena, and because elephants have been shown to select shaded habitats during peak temperatures (Kinahan *et al.* 2007a), we expect elephants to move towards to the lower parts of the catena during periods of high temperatures, and move up the catenary gradient during cooler periods.

In this paper, we focus on the influence of catenary topography on the seasonal and circadian patterns of terrain-use by elephants in a South African savanna system, namely Kruger National Park and adjacent nature reserves. We test the hypotheses that elephants (1) move progressively down slope during seasonal dry periods, and (2) move to lower parts of the catena during times of peak temperature (i.e., midday), going back to higher parts of the catena during cooler periods of the day. We relate the patterns of terrain-use by the elephants to seasonal variation in rainfall and circadian rhythms of temperature. Through explicitly focusing on these issues, we aim at increasing our understanding of the way topo-edaphic conditions influence the distribution of elephants.

Methods

Study area and species

Kruger National Park is South Africa's largest nature reserve, which, together with its adjacent nature reserves to the west (i.e., Balule, Klaserie, Manyeleti, SabiSand, Timbavati and Umbabat), encompasses some 21700 km^2. The rainfall pattern is typical of southern African savannas, with a wet season from November to March, and a dry period over the rest of the year (Witkowski & O'Connor 1996). Granitic rocks in the west and basaltic rocks in the east underlie the majority of the study area, and catenas manifest very important ecological systems here (Venter *et al.* 2003). For an extensive description of the abiotic landscape template and its associated vegetation pattern in the study area, see Venter *et al.* (2003).

We used data from 43 elephants fitted with global positioning system (GPS) collars (Hawk105 collars, Africa Wildlife Tracking cc., South Africa) that recorded their locations

at hourly intervals over a 3 year period (2005-2008). This resulted in 516,771 locations being recorded, with a positional precision of ≤ 27.8 m in 95% of the records.

Terrain analyses

We used the void-free Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) of 3 arc-second horizontal resolution (ca. 80 m in our study area), and a vertical resolution of 1 m (Rodriguez *et al.* 2006; Jarvis *et al.* 2008). This DEM constitutes about the finest resolution and most accurate topographic data available for most of the globe (Rodriguez *et al.* 2006; Rennó *et al.* 2008). Prior to analyses, we removed single-cell pits and peaks, since these often represent artefacts in the data (Rennó *et al.* 2008). Altitudes in the study area ranged from 107 to 836 m a.s.l.

To represent the catenary topography of the study area, we calculated the topographic position of each grid cell relative to the highest and lowest locations within a circular neighbourhood around the grid cell (LEP: local elevation percentile). Low LEP values indicate relatively low-lying areas (e.g., valley bottom and bottom slope), whereas high LEP values indicate a high local elevation (e.g., crests or peaks).

Like most topographic indices, LEP is sensitive to the spatial scale of analysis, i.e., the extent of the neighbourhood considered for the computation of local minimum and maximum altitudes (Fisher *et al.* 2004; Schmidt & Andrew 2005; A-Xing *et al.* 2008). Hence, to adequately quantify the structure of land-surfaces, topographical indices should be computed at multiple scales (Li & Wu 2004). We therefore computed the LEP for each grid cell using four different spatial scales (i.e., radii of the moving window): a neighbourhood up to 5, 12, 25 or 50 grid cells (corresponding respectively to 400 m, 960 m, 2 km and 4 km horizontally). The computation of LEP at the different spatial scales was done using the software TAS (Lindsay 2005, 2006).

Furthermore, we averaged the LEP values over these scales considered, to yield a multiscale composite index of local topographic position. A visual representation of the
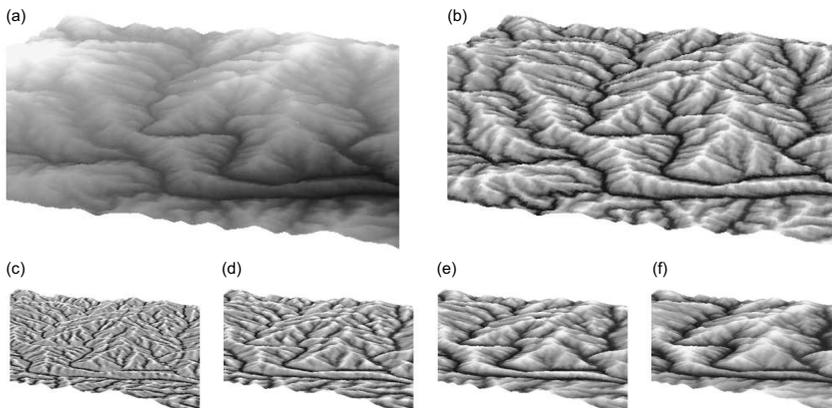

Figure 2.1: (a) Elevation and (b) local elevation percentile averaged over all scales considered, as well as per scale individually: (c) 5, (d) 12, (e) 25 and (f) 50 cells. Note that the figures are displayed with 10 times vertical exaggeration to facilitate visual interpretation. Black shading indicates low values, whereas white shading indicates high values.
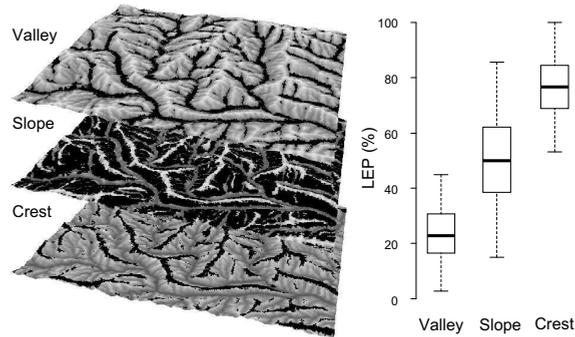
Figure 2.2: Relationships between local elevation percentile (LEP) and landform, classified as "valley", "slope" or "crest" and indicated in black shading in the maps. Note that the figures are displayed with 10 times vertical exaggeration to facilitate visual interpretation.

influence of the spatial scale considered in computing LEP is given in Figure 2.1. Small neighbourhoods for the computation of LEP highlight small-scale undulations in the landscape (Fig. 2.1c), whereas larger neighbourhoods show only larger valleys and crests (Fig. 2.1f). The composite mean LEP over the four scales considered includes the effects of undulations at various scales (Fig. 2.1b).

To verify that LEP provides meaningful information regarding the position of a site along the catenary sequence, we associated the LEP values to frequently used landform classes. Many landform classifications follow a 6-classes scheme: peak, pass, pit, plane, channel and ridge (Fisher *et al.* 2004). We classified the surface of our study area into these classes, using the multiscale approach as outlined by (Fisher *et al.* 2004) and implemented in the software package LandSerf (Wood 2009b,a). We combined pits and channels into one class representing the valley bottom, planar surfaces represented the slopes of the catena, and peaks and ridges were combined to into one class representing the crest of the catena. Analysis of the relationships between LEP and these classes confirmed that LEP quantifies the relative topographic position of each site in the study area along a gradient from valley bottom to crest (Fig. 2.2). Because the classification of sites into landforms assumes homogeneity within each class, while our index is continuous, LEP shows variation within each class (Fig. 2.2).

Analyses

We analysed the patterns of terrain-use by elephants along the catenary gradient through comparing the LEP values associated to the visited locations (the "used" sites) to the distribution of LEP values in the study area. We considered the area within 1 km from the recorded GPS positions to be available to the elephants (i.e., the "reference area" or "available sites"). To analyse whether the elephants were distributed nonrandomly regarding LEP, we compared the distribution of LEP values of these used sites to that of the available sites, expressed in terms of marginality and specialization (Hirzel *et al.* 2002). The marginality expresses the deviance of the mean of the distribution of LEP regarding the used sites (the species mean) from the mean of the distribution of LEP values in the reference area (the global mean) (Hirzel *et al.* 2002). Specialization expresses the

width of the distribution of LEP values used by the elephants relative to that of the global distribution.

Following Hirzel *et al.* (2002), we calculated marginality (M) as the difference between the species mean (m_s) and global mean (m_g), divided by 1.96 standard deviations (σ_g) of the global distribution:

$$M = \frac{m_s - m_g}{1.96 \, \sigma_g} \qquad (2.1)$$

Division by σ_g is needed to remove any bias introduced by the variance of the global distribution, and the coefficient weighting σ_g (1.96) ensures that $|M|$ will mostly be between zero and one, where a large value of $|M|$ means that the elephants live in very particular conditions relative to the reference area (Hirzel *et al.* 2002). Negative values of M indicate that the elephants select LEP values lower than m_g and positive values indicate that the elephants select LEP values higher than m_g (Hirzel *et al.* 2002). Specialization (S) was calculated as the ratio between σ_g and the standard deviation of the species distribution regarding LEP (σ_s):

$$S = \frac{\sigma_g}{\sigma_s} \qquad (2.2)$$

High values of S indicate that the species distribution regarding LEP is much narrower than the global distribution regarding LEP.

To test our hypotheses, we related the patterns of terrain-use, as quantified by M and S for LEP, to seasonal fluctuations in rainfall and within-day temperature fluctuations. Data on daily rainfall was obtained from several weather stations in the study area. Because rainfall was very erratic, we used a 60-day moving average to represent the seasonality in rainfall (Fig. 2.3a). We obtained temperature data from a temperature logger placed in open vegetation, thus representing the temperature in open field exposed to solar radiation. This sensor recorded the temperature throughout the day at a 30-minute interval and an 83-day period (1/9/2007 - 22/11/2007). Furthermore, besides recording the elephants' positions, the GPS collars were also equipped with temperature loggers, measuring the temperature as experienced by the elephants.

For a 30-day moving window from December 2005 until October 2008, we calculated M and S and related these indices to the average rainfall in the 60 days prior to the observational window. For the within-day analyses, we calculated M and S per hour over the 83-day period during which data was obtained from the temperature sensor. However, we also pooled all the data to get an overall picture of M and S per hour of the day. All analyses were conducted using the software R (R Development Core Team 2009).

Results

The results showed a strong seasonal and within-day pattern of the marginality M, yet not of the specialization S. The values of S were mostly very low (< 1.3), indicating that the distribution of LEP values of the recorded elephant locations was not particularly narrow relative to the global distribution of LEP values in the study area. This indicates that the elephants used all the sites along the catenary gradient, and not systematically avoided certain areas. We therefore focus on the seasonal and daily patterns of M. Moreover, the composite mean LEP over all the scales considered showed more pronounced

seasonal and daily patterns of M than each of the scales considered individually. We therefore present only the results for this multiscale composite mean LEP.

Overall, the elephants slightly preferred to be at the lower part of the catena ($M = -0.131$). However, the importance of topographic position increased when including seasonal and within-day fluctuations (Fig. 2.3 and 2.4). Over time, the fluctuation in M showed a pattern that largely resembled that of seasonality in rainfall (Fig. 2.3). Especially in the late dry season (September and October), the elephants were on average (i.e., over the entire day) found at distinctly lower parts of the catena ($M \approx -0.3$) than in wet periods ($M > -0.1$) (Fig. 2.3).

However, independent of this seasonal fluctuation in terrain-use along the catenary gradient, the elephants predominantly used different parts of the catena during different periods within a day (Fig. 2.4). These within-day patterns closely matched the pattern of temperature throughout the day, where the elephants moved to lower parts of the catena when the temperature was high (Fig. 2.4). This pattern was consistent throughout the year, yet in absolute terms influenced by the seasonal pattern (Fig. 2.3).

Relating M directly to rainfall and temperature data (stratified with classes of 0.1 °C or 0.1 mm/day, respectively) confirmed that the elephants moved to lower parts of the catena during times with only scarce rainfall (especially < 2 mm/day; Fig. 2.5a), and when temperature was high (Fig. 2.5b). The magnitude of the effect of temperature was much higher than that of rainfall ($M \approx -0.6$ when the temperature is high, vs. $M \approx -0.25$ during dry periods; Fig. 2.5). Comparing the temperature as gauged by the GPS collars on the elephants to the temperature gauged by the sensor in the open field showed that the higher the midday temperature in the open field, the lower (in relative
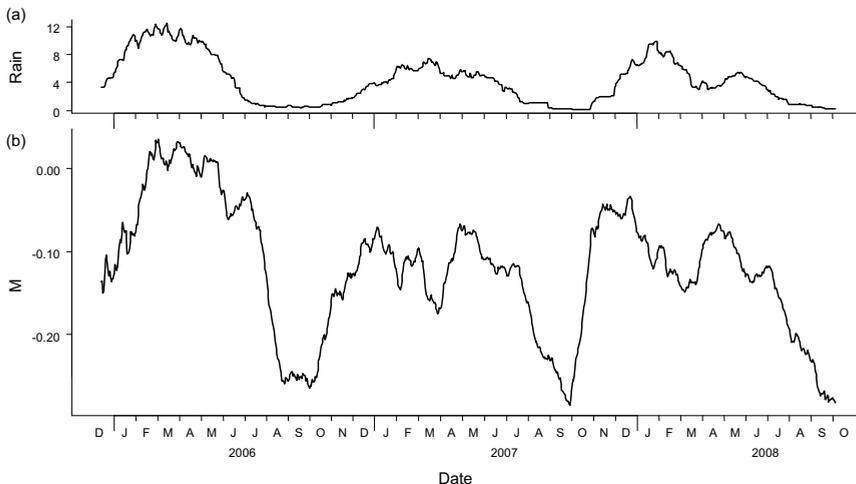
Figure 2.3: (a) Rainfall (in mm/month) during the study period, measured as a 60-day moving average, and (b) the marginality (M) for the local elevation percentile (LEP) of the sites visited by the elephants relative to the average conditions in the study area. A value of zero means that the elephants are, on average, found in sites similar to the mean conditions in the study area, while negative values indicate that the elephants predominantly visited sites associated to low LEP values, thus sites at the lower end of the catenary gradient.
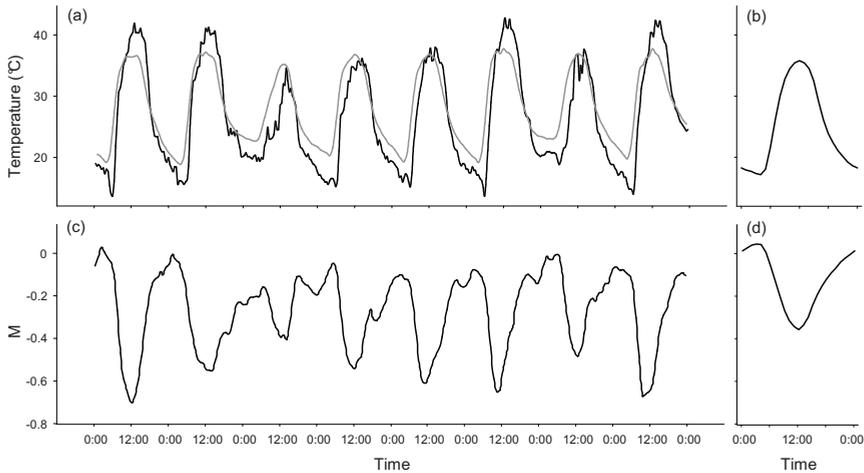
Figure 2.4: (a) Temperature gauged by the temperature sensor positioned in the field (black line) as well as GPS collar (grey line) between the 5th and 13th of September 2007 and (b) the average pattern of temperature throughout the day. (c) The marginality (M) for local elevation percentile (LEP) of the sites visited by the elephants relative to the average conditions in the study area. A value of zero means that the elephants are, on average, found in sites similar to the mean conditions in the study area, while negative values indicate that the elephants predominantly visited sites with low LEP values, thus sites at the lower end of the catenary gradient. The time frame displayed equals the period indicated above. (d) The average pattern of M throughout a day, averaged over the entire study period.

terms) the temperature as measured by the GPS collars at the locations of the elephants (Fig. 2.5c). During the night, there was only a weak correlation, with the GPS collars measuring slightly higher temperatures (Fig. 2.5d).

Discussion

In this paper, we investigate the influence of catenary topography on the distribution of African elephants in a South African savanna system, and tested the hypotheses that elephants move progressively to lower parts of the catena with the advance of the dry season and move down slope during times of peak temperature. Our results demonstrate that elephants facultatively alter their behaviour in ways that are consistent with our hypotheses, showing pronounced seasonal and circadian rhythms of terrain-use.

We are not the first to demonstrate seasonal movements of animals along the catenary gradient, since this has been shown for several grazing (Bell 1971) and browsing herbivores (Pellew 1984; Venter *et al.* 2003). Our findings complement these studies. These seasonal patterns mainly relate to the abundance and quality of vegetation, influenced by the patterns of rainfall and the relative topographic position of a site. As such, the local topography and large-scale climatic conditions interact to influence the patterns of terrain-use by large herbivores.

However, in addition to this seasonal trend in terrain-use, our study highlights a circadian rhythm of terrain-use by elephants along the catenary gradient, a pattern that, to our knowledge, has not been shown before. The elephants moved progressively down the catena towards midday, when the solar insolation is most profound and temperatures
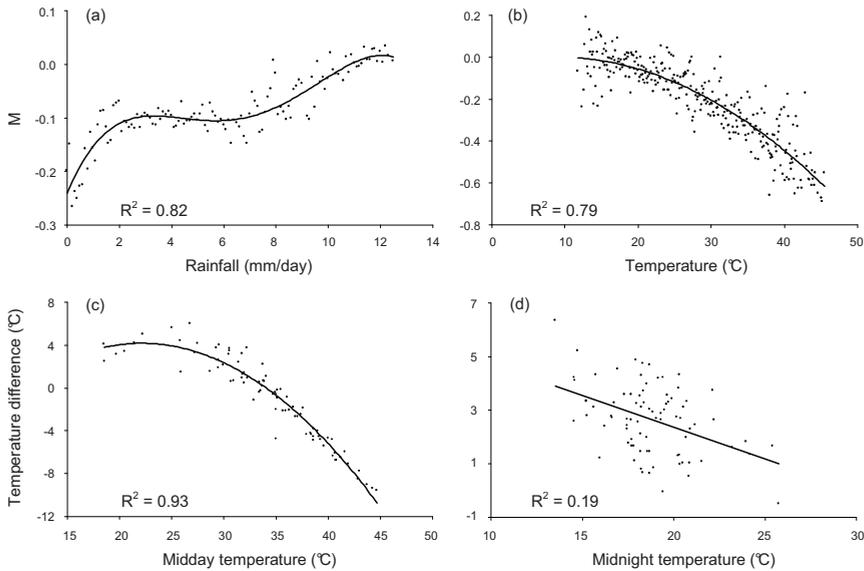
Figure 2.5: The marginality (*M*) for local elevation percentile (LEP) in relation to (a) the average amount of rainfall during the preceding 60 days and (b) the temperature as measured by a temperature sensor placed in the open field. The difference between the temperature measured by the GPS collars and the temperature sensor in the open field during (c) midday and (d) midnight. Negative values indicate that the temperature gauged by the GPS collar, thus experienced by the elephant, is lower than the temperature measured by the sensor in the field. The R^2 values are based on polynomial linear regression (a: 4th order; b and c: 2nd order; and d: 1st order).

are highest. Because the lower lying parts of the catena generally have a higher canopy cover (Du Toit 2003; Asner *et al.* 2009) and because elephants may face physiological problems of dissipating heat during spells of extremely high temperature (Kinahan *et al.* 2007a), moving to the lower parts of the catena during midday may be one way in which the elephants adapt their daily rhythms to the thermal constraints their large sizes impose on them.

Our results showed that the higher the ambient temperature as gauged by a sensor in the open field, the lower, on average, the elephants were found along the catena. Moreover, the temperature recorded by the GPS collars, representing the temperature as experienced by the elephants, decreased relative to an increasing temperature in the open field, suggesting that the elephants increasingly found shade when the temperature and level of solar energy input increased. Because shade is more abundant in the lower parts of the catena (Du Toit 2003; Asner *et al.* 2009), seeking shade by progressively moving downward when the temperature rises thus probably is the cause of the observed patterns (Kinahan *et al.* 2007a).

Regardless of the exact mechanism at work, it was clear that the elephants repositioned themselves relatively low in the landscape during August-October, but also year-round during midday. Although we used field data and correlative analyses, we contend that these patterns of terrain-use by elephants are ultimately driven by cyclic patterns in rainfall (seasonal) and temperature/solar radiation (circadian), where the circadian pat-

terns have a stronger influence on elephant terrain-use than the seasonal patterns (see Fig. 2.3, 2.4 and 2.5). The circadian patterns directly impact elephants through heat stress (Kinahan *et al.* 2007a,b), while the seasonal pattern of rainfall indirectly influences the distribution of elephants through influencing the quantity and quality of food resources along the catenary gradient (Bell 1971; Nellemann *et al.* 2002; Venter *et al.* 2003). Thus, through different processes operating at different time scales, the topography in our study area has a profound influence on the ecology of elephants. However, although relative topographic position proved to be an important determinant of the spatial distribution of elephants at specific periods in a year or day, the elephants were rather indifferent about topographic position during times of abundant, high quality resources (i.e., during the wet season) or when heat stress was not an issue (i.e., during the night).

These findings highlight the importance of considering local topography in studies on the biogeographical patterns of species abundances: a given site (e.g., valley) at 200 m a.s.l. might have a similar environment as another site at 650 m a.s.l., while at 200 m a.s.l. one can find a range of different local environments (e.g., valley, slope, crest) (Rennó *et al.* 2008). In other words, it might not be elevation *per se* that is driving the processes behind the observed (spatial) patterns, and catenary topography might give more insight into system behaviour. Notwithstanding, elevation *per se* often correlates with large-scale climatic conditions, so that elevation may influence biogeographical patterns indirectly through climate (Korner 2007). Although there may historically have been benefit for the elephants in our study area in migrating west during dry periods, up the rainfall gradient toward South Africa's eastern escarpment, this option is now largely precluded by fences, roads, and incompatible land-use (Venter *et al.* 2003). What remains are local topographical gradients with their associated abiotic template and vegetation pattern, influencing the seasonal and circadian patterns of terrain-use by elephants.

Besides focusing attention to the importance of the scale of topography in the study of biogeographical patterns, this study highlights the importance of temporal scale when studying habitat selection by elephants. As Boyce (2006) argues, variation in processes over different time scales can generate distinctive patterns that are overlooked or misunderstood when viewed from an inappropriate temporal resolution or extent. In our study, the circadian cyclic patterns of terrain-use in relation to the catenary gradient would not have been found if we did not analyse the data at sufficiently fine temporal resolution (i.e., sufficiently finer than a day). Moreover, we would not have found these circadian patterns had we analysed the data using elevation only. Hence, for processes to be studied, one has to view a system at appropriate spatial and temporal scales while explicitly considering the context within which processes and interactions occur (Van Langevelde 2000; Gutzwiller & Riffel 2007; De Knegt *et al.* 2010). Hence, even when data are collected and analysed at a sufficiently fine temporal resolution, the patterns to be found depend on the spatial perspectives chosen. Thus, conclusions that habitat preference is not a function of time of day (e.g., Ntumi *et al.* 2005, in a study on elephant distribution in the Maputo Elephant Reserve, Mozambique) may be an artefact of the analyses by not explicitly considering the influence of fine-scaled spatial patterns in topography.

Our findings help to understand the links between the abiotic template and its associated vegetation pattern in relation to stress and resource gradients on the one hand, and the patterns of terrain-use by elephants on the other hand. We have shown that elephant terrain-use is characterized by seasonal and circadian rhythms, and differentially distributed along topographically mediated environmental gradients in ways that

are consistent with known ecophysiological processes. Depending on the climatic conditions and time of the day, the elephants preferred to be predominantly at the lower parts of the catena, while being distributed indifferently over the catenary gradients at other times. This may be the reason why Asner *et al.* (2009) recently found the woody vegetation in our study area, at the lower parts of the catena to be more heavily impacted by elephants, or large herbivores in general, than the woody vegetation in the upland part of the catena. Understanding the relationships between the fine-scale topography and habitat selection by large herbivores is thus essential to understand biotic change, not only in savanna ecosystems as illustrated in this paper, but also in other systems such as (hemi)boreal (e.g., Mysterud 1999) and arctic (e.g., Szor *et al.* 2008). We conclude that fine-scale topography is important in explaining species distributions, because it interacts with large-scale climatic variation to mediate the distribution of resources and abiotic conditions over the landscape.

HJ de Knegt, TA Groen, CADM van de Vijver, HHT Prins & F van Langevelde

3

Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning

Here, we address the question whether and through which mechanisms herbivores can induce spatial patterning in savanna vegetation, and how the role of herbivory as a determinant of vegetation patterning changes with herbivore density and the pre-existing pattern of vegetation. We thereto developed a spatially explicit simulation model, including growth of grasses and trees, vertical zonation of browseable biomass, and spatially explicit foraging by grazers and browsers. We show that herbivores can induce vegetation patterning when two key assumptions are fulfilled. First, herbivores have to increase the attractiveness of a site while foraging so that they will revisit this site, e.g., through an increased availability or quality of forage. Second, foraging should be spatially explicit, e.g., when foraging at a site influences vegetation at larger spatial scales or when vegetation at larger spatial scales influences the selection and utilisation of a site. The interaction between these two assumptions proved to be crucial for herbivores to produce spatial vegetation patterns, but then only at low to intermediate herbivore densities. High herbivore densities result in homogenisation of vegetation. Furthermore, our model shows that the pre-existing spatial pattern in vegetation influences the process of vegetation patterning through herbivory. However, this influence decreases when the heterogeneity and dominant scale of the initial vegetation decreases. Hence, the level of adherence of the herbivores to forage in pre-existing patches increases when these pre-existing patches increase in size and when the level of vegetation heterogeneity increases. The findings presented in this paper, and critical experimentation of their ecological validity, will increase our understanding of vegetation patterning in savanna ecosystems, and the role of plant-herbivore interactions therein.

Introduction

Savanna ecosystems, characterised by a continuous layer of grass intermixed with a discontinuous layer of trees and shrubs, are among the most striking vegetation types where contrasting plant life forms co-dominate (Scholes & Archer 1997). Factors regulating the balance between these life forms include rainfall, soil type, disturbances (e.g., herbivory and fire) and their interactions (Greig-Smith 1979; Huntley & Walker 1982; Archer 1990; Scholes & Walker 1993). Savanna vegetation is spatially heterogeneous and often shows patterning, frequently a two-phase pattern of discrete shrub or tree clusters scattered throughout grassland (Archer *et al.* 1988; Archer 1990; Couteron & Kokou 1997; Breshears 2006). Understanding the origin of such vegetation patterns is a central issue in ecology (Greig-Smith 1979; Jeltsch *et al.* 1996; Sankaran *et al.* 2004, 2005), for vegetation patterning can have important consequences for ecosystem functioning (Adler *et al.* 2001; Rietkerk *et al.* 2004). At broad spatial scales, the key determinants of patterning in savanna vegetation include spatial differences in abiotic characteristics such as rainfall and nutrient availability (Greig-Smith 1979; Huntley & Walker 1982; Scholes & Walker 1993). On the other hand, herbivory, fire, surface-water run-on and runoff processes and soil nutrient-organic matter dynamics are considered as important determinants of vegetation patterning at finer scales (Greig-Smith 1979; Huntley & Walker 1982; Scholes & Walker 1993; Jeltsch *et al.* 1996, 1998; Van de Koppel & Prins 1998; Klausmeier 1999; HilleRisLambers *et al.* 2001; Lejeune *et al.* 2002; Sankaran *et al.* 2004, 2005). However, the mechanisms behind spatial vegetation patterning in savannas are still poorly understood (Jeltsch *et al.* 2000; Weber & Jeltsch 2000; Sankaran *et al.* 2004, 2005).

Albeit several mechanisms underlying patterning in savanna vegetation have been proposed [e.g., diffusion driven instabilities: Rietkerk *et al.* (2002a), Rietkerk *et al.* (2004), Kéfi *et al.* (2007), Scanlon *et al.* (2007), and disturbance by fire: Van de Vijver *et al.* (1999), Van Langevelde *et al.* (2003)], the potential influence of herbivores on the spatial component of savanna vegetation remains obscure (Scholes & Archer 1997; Jeltsch *et al.* 2000; Weber & Jeltsch 2000; Lejeune *et al.* 2002; Sankaran *et al.* 2004, 2005). Since savannas support a large proportion of the world's human population and a majority of its rangeland and livestock (Scholes & Archer 1997), understanding the role of herbivores in vegetation patterning in these ecosystems is urgently required (Sankaran *et al.* 2005), moreover because savannas are among the ecosystems that are most sensitive to future changes in land use and climate (Sala *et al.* 2000; Bond *et al.* 2003; House *et al.* 2003).

In this paper, we therefore focus on the mechanisms through which herbivores induce or modify spatial patterning in savanna vegetation. We do this by modelling herbivore-vegetation interactions in a spatial context and analysing the key assumptions that are required for herbivores to induce spatial patterning. We focus on two basic mechanisms of plant-herbivore interactions that we consider important for vegetation patterning to occur: self-facilitation and spatial dependency of foraging. Self-facilitation is the process where herbivores increase the attractiveness of a site while foraging. This process occurs when herbivory enhances the quality or quantity of regrowth following defoliation. The former has often been observed when nutrient concentration is increased in post-defoliation regrowth through the replacement of older, low-quality leaves by younger, high-quality tissue (Anderson *et al.* 2007). The latter applies when herbivory leads to an increased amount of regrowth following defoliation or adjustment of the vertical stratification of forage material, thereby influencing the availability of reachable forage (Fornara

& Toit 2007). Spatial dependency of foraging is the process where the interaction of herbivory with vegetation at a site is influenced by the surroundings of the site. For example, vegetation characteristics at larger spatial scales can influence the selection of sites to forage (Senft *et al.* 1987). Accordingly, the surrounding matrix of a site can be positive (attractive) or negative (repellent) in the herbivore's choice of a particular site (Baraza *et al.* 2006). Moreover, herbivores do not only forage strictly in selected sites, but also in the close surroundings of that site (Cid & Brizuela 1998; Adler *et al.* 2001; Baraza *et al.* 2006).

We include these processes in our modelling exercise because they are mentioned in many studies on herbivore foraging in relation to pattern formation (Prins & Van der Jeugd 1993; Cid & Brizuela 1998; Adler *et al.* 2001; Woolnough & Du Toit 2001; Baraza *et al.* 2006; Fornara & Toit 2007). By analysing the conditionality of these processes for vegetation pattern formation to occur, we try to increase our understanding of the mechanisms through which herbivores induce spatial patterning in savanna vegetation. Additionally, we analyse the effects of herbivore density and the initial landscape configuration on the role of herbivores in vegetation patterning. Focusing only at the influence of herbivory while leaving out other determinants like fire, nutrient cycling or water redistribution and their possible interactions allows us to isolate the effect herbivores can have on vegetation patterning. Hence, we aim at contributing to a better understanding of the role of herbivory as a determinant of spatial vegetation patterning in savanna ecosystems.

The model

Model overview

We developed a spatially explicit, cell-based model that simulates vegetation dynamics in each cell based on the availability of and competition for resources between grasses and trees. We then introduce herbivores into the simulated landscape, both grazers, foraging only on grass, and browsers, foraging exclusively on trees. The spatial pattern of biomass removal through herbivory is modelled to be determined by the spatial distribution of the herbivores. Through varying parameter values, we analyse the influence of herbivory on vegetation patterning. Our simulations are run in a landscape covering a lattice with 200 x 200 cells of 5 x 5 m each. To avoid edge effects, the simulated landscape is torus-shaped. The maximum time span of each simulation run is 1000 annual time steps, but the simulation is finished when the state variables remain constant for 50 years. The processes, variables and parameters (Table 3.1) involved are discussed below, in order of appearance of the three main components in the flow of the model: resource availability, vegetation dynamics and herbivory. We then outline the methods of model analyses and scenarios that are simulated.

Resource availability

Following the majority of models that study savanna tree-grass dynamics (Walter 1971; Walker *et al.* 1981; Walker & Noy-Meir 1982; Eagleson & Segarra 1985; Higgins *et al.* 2000; Van Wijk & Rodriguez-Iturbe 2002; Fernandez-Illescas & Rodriguez-Iturbe 2003; Van Langevelde *et al.* 2003), we consider available moisture as the main resource limiting plant growth and neglect competition for nutrients. We used the two-layer hypothesis (Walter 1971) as the basis for water distribution in the soil and availability for tree and grass growth. This hypothesis assumes niche separation in the rooting zone of grasses

Table 3.1: Parameters used in the model and their interpretation.

Name	Interpretation	Units	Values	Sources
w_{in}	Annual amount of infiltrated water	mm	560	
α	Proportion of excess water that percolates to the tree root zone	-	0.4	De Ridder & van Keulen (1995)
β	Soil moisture content in the grass root zone above which water starts to percolate to the tree root zone	$\frac{mm}{m^2}\,yr^{-1}$	350	De Ridder & van Keulen (1995)
r_H	Water use efficiency of grass biomass	g mm^{-1}	1	Gambiza *et al.* (2000)
r_W	Water use efficiency of woody biomass	g mm^{-1}	0.5	Le Houérou (1980)
θ_H	Rate of water uptake per unit grass biomass	$\frac{mm}{yr}\,g^{-1}$	0.9	Walker *et al.* (1981)
θ_W	Rate of water uptake per unit woody biomass	$\frac{mm}{yr}\,g^{-1}$	0.5	Walker *et al.* (1981)
d_H	Specific loss of grass biomass due to mortality	yr^{-1}	0.9	Gambiza *et al.* (2000)
d_W	Specific loss of woody biomass due to mortality	yr^{-1}	0.4	Le Houérou (1980)
h_t	Total height	m	0.5-10	
h_b	Canopy bottom height	m	1/3 h_t	
h_m	Canopy midpoint height	m	2/3 h_t	
c_w	Canopy width	m	3/4 h_t	
I_{in}	Index value for the incident light intensity above the canopy	-	1	
k	Light extinction coefficient of browseable biomass	-	0.2	Huisman *et al.* (1997)
f_d	Yearly food intake as proportion of body mass	-	9.125	Owen-Smith (2002)
G	Grazer density	g m^{-2}	1.0	
B	Browser density	g m^{-2}	0.1	
λ	Amount of forage removed by the herbivores from a selected cell in each iteration of the foraging loop	g	500	
i_{max}	Maximum food intake rate at high food abundance	g min^{-1}	20	Owen-Smith (2002)
$g_{\frac{1}{2}}$	Food availability at which I reaches half of its maximum	g m^{-2}	100	Owen-Smith (2002)
q	Coefficient of the decrease in grass quality with increasing standing biomass	-	0.0019	Prins & Olff (1998)
$bhmax$	Maximum reachable height of the browsers	m	5	
adj	Proportion of λ that is removed from adjacent cells	-	0.1	
wf	Exponent for the weighting of a cell	-	-3	

and trees. Grasses are the superior competitors for moisture in the topsoil layer (i.e., grass root zone), where both grasses and trees have roots. In the subsoil layer (i.e., tree root zone), the competitive ability of trees is dominant, since only a negligible proportion of the grass roots penetrate to this depth (Weltzin & McPherson 1997; Schenk & Jackson 2002). Following Van Langevelde *et al.* (2003), we assume that all water that infiltrates in the soil on a yearly basis is available for the growth of grasses and trees. This infiltrated water first increases the soil moisture content in the grass root zone. Above a certain threshold, water starts to percolate from the grass root zone into the tree root zone. We assume that both rooting zones are not water saturated in savannas. The recharge rate of moisture in the grass root zone (w_t) can then be given by:

$$w_t = w_{in} - w_s \qquad (3.1)$$

where w_{in} is the amount of infiltrated water per year and w_s is the rate of moisture recharge in the tree root zone (Van Langevelde *et al.* 2003). The parameter w_s is propor-

tional to the amount of infiltrated water:

$$w_s = \alpha(w_{in} - \beta) \quad \text{if} \quad w_{in} > \beta \quad \text{else} \quad w_s = 0 \tag{3.2}$$

where β is the soil moisture content in the grass root zone above which water starts to percolate to the tree root zone, and α is the proportion of excess water above β that percolates to the tree root zone.

Vegetation dynamics

The model features the vegetation components grass biomass (H, consisting of grasses and herbs) and woody biomass (W, consisting of wood, twigs and leafs of trees and shrubs). The rate of change of aboveground grass biomass over one year can be calculated as follows (Walker *et al.* 1981; Walker & Noy-Meir 1982; Van Langevelde *et al.* 2003):

$$\frac{dH}{dt} = r_H \, w_t \frac{H \, \theta_H}{H \, \theta_H + W \, \theta_W + w_S} - d_H \, H - L_{HH} \tag{3.3}$$

where r_H is the water use efficiency of grass, θ_H and θ_W the rates of water uptake per unit biomass of grasses and trees, respectively, d_H the specific loss of grass biomass due to mortality and senescence, and L_{HH} the loss of herbaceous biomass due to grazing. The rate of change of woody biomass over one year can be represented by:

$$\frac{dW}{dt} = r_W w_t \frac{W \, \theta_W}{H \, \theta_H + W \, \theta_W + w_S} - d_W \, W - L_{WH} \tag{3.4}$$

where r_W is the water use efficiency of trees, d_W the specific loss of woody biomass due to mortality and senescence, and L_{WH} the loss of woody biomass due to browsing (Van Langevelde *et al.* 2003). Without herbivores, grasses are able to dominate when the amount of infiltrated water is below β (Walker & Noy-Meir 1982). Trees and grasses co-occur when the amount of infiltrated moisture is above this threshold and below the availability at which trees start dominating the vegetation. With increasing moisture availability, the vegetation thus shows transitions from grassland to savanna to woodland (Walker & Noy-Meir 1982; Van Langevelde *et al.* 2003).

Since the vertical structure of woody biomass determines the herbivores' access to browse, we expanded the two-dimensional vegetation model as described above with the vertical dimension. For simplicity, our model does not track individual trees, but rather height cohorts of identical individuals. Twenty cohorts (that can co-occur in a single cell) represent the vertical structure of the woody vegetation. A cohort is defined here as a group of individual trees with the same height and other characteristics (e.g., size and shape, all being an allometric function of tree height). The shortest cohort contains trees of 0.5 m in height and subsequent cohorts increase in height with 0.5 m increments up to the tallest cohort of 10 m tall trees. Trees of each cohort are characterised by their height (h_t), canopy bottom height (h_b), canopy midpoint height (h_m), canopy width (c_w), total aboveground biomass and a browseable/non-browseable biomass allocation ratio, where large trees have proportionally less browseable biomass than small trees. Browseable biomass is the part of the plant that is eaten by browsers and consists mainly of leaves, but could contain a small proportion of branches. To provide an idealised canopy geometry that closely mimics the shape of a typical savanna tree crown (Caylor

et al. 2004), canopy width at each layer d in the canopy ($c_{w,d}$), with $h_b < d < h_t$, is modelled as:

$$
\begin{aligned}
c_{w,d} &= \sqrt{c_w^2 \left(1 - \frac{(d - h_m)^2}{(h_t - h_m)^2}\right)} && \text{if} \quad d - h_m \geq 0 \\
c_{w,d} &= c_w \exp\left(4\frac{d - h_m}{h_m}\right) && \text{if} \quad d - h_m < 0
\end{aligned}
\tag{3.5}
$$

With the total biomass of each cohort in a cell, the browseable biomass is calculated for each cohort and the vertical zonation of all browse in a cell is calculated for height layers with 0.5 m increments. Multiple cohorts can thus contribute browseable biomass to a single height layer.

Due to growth, trees in a cohort can shift to the next cohort. This increases the total biomass of that cohort, and thus the total woody biomass in the cell. Due to mortality, woody biomass is removed from a cohort, thereby decreasing the total woody biomass in the cell. These two processes, i.e., growth and mortality, are operating simultaneously in each cell, resulting in a change of biomass as calculated with Eq. 3.4. The change in biomass is allocated to the different cohorts as a function of the amount of intercepted light per cohort. Growth is modelled to be positively related to the amount of intercepted light per cohort, while for mortality and senescence the relation is negative. Thus, cohorts that intercept a lot of light largely contribute to the increase of woody biomass and experience only small losses. The light intensity at each layer d in the canopy (I_d) is calculated using the Lambert-Beer equation:

$$
I_d = I_{in}\,e^{-k\,W_{b,d+}}
\tag{3.6}
$$

where I_{in} is the incident light intensity above the canopy, k is the light extinction coefficient and $W_{b,d+}$ is the total amount of biomass above layer d (Huisman *et al.* 1997). The amount of intercepted light of cohort c (Int_c) is subsequently calculated as:

$$
Int_c = \sum_{d=0}^{h_t} \left[I_{in}\,e^{-k\,W_{b,d+}}(1 - e^{-k\,W_{b,c,d}})\right]
\tag{3.7}
$$

were $W_{b,c,d}$ is the amount of biomass of cohort c at layer d. Trees in the highest cohort do not grow since they are assumed to have reached their maximum size. Likewise, biomass gain due to regeneration is kept at a constant proportion of the change in woody biomass as calculated with Eq. 3.4. Consequently, without disturbance such as browsing, the woody biomass in a cell grows to the equilibrium standing biomass, consisting exclusively trees in the highest cohort (Fig. 3.1).

Herbivory

The browser and grazer populations are simulated as herds that can move freely in the landscape and have complete knowledge regarding the distribution of their food resources. Using an ideal free distribution approach (Fretwell & Lucas 1970), herbivores select cells to forage based on the attractiveness of cells. If several cells have the same attractiveness, the herbivores choose one of the cells at random. Within the yearly simulation loop for plant growth, a foraging loop is implemented. In each step of the foraging
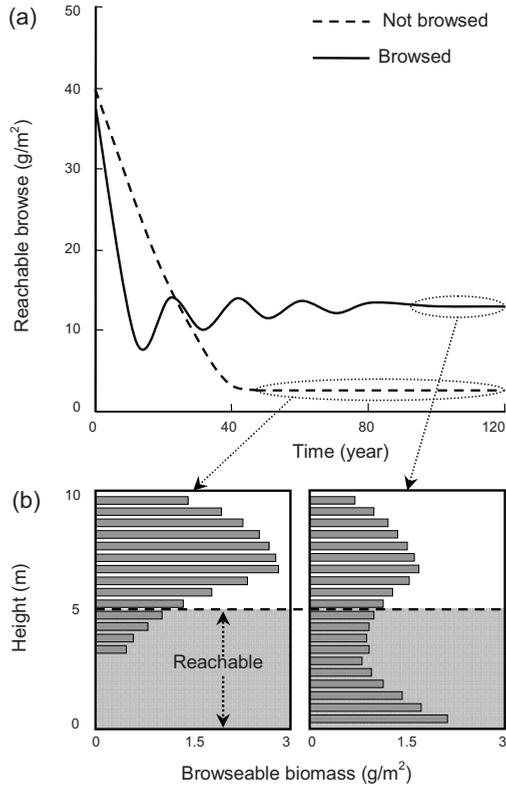
Figure 3.1: (a) Dynamics of reachable browseable biomass (i.e., browse between 0-5 m high) in a cell for a scenario without (dashed line) and with browsing (continuous line) for an initial situation where all cohorts have an equal amount of biomass. (b) Vertical stratification of browseable biomass with and without browsing after the system stabilised. Although browsing removes biomass in the short term, it stimulates regrowth and regeneration and thereby enhances the amount of reachable browse by keeping the trees short.

loop, the attractiveness of all cells is calculated, and the cell with the highest attractiveness is selected. The herbivores remove λ gram of biomass from the selected cell, and then the next foraging step follows. The foraging loop continues until the requirements of the herbivore population are met and the total amount of forage consumed in a cell determines L_{HH} (Eq. 3.3) and L_{WH} (Eq. 3.4) for each cell in the simulated landscape.

In the analysis of the effect of herbivory on vegetation patterning, the population sizes were kept constant. Although it is obvious that a constant population size does not hold in large natural systems, we used this assumption because (1) the study was performed in a relatively small area and, more importantly, (2) because we want to isolate the effect of herbivory on vegetation patterning and do not want to include interactive effects of herbivore dynamics. The yearly population food requirement (req_p) is calculated as:

$$req_p = f_d \, p_{size} \tag{3.8}$$

where f_d is the yearly food intake as proportion of the body mass of the foragers and p_{size}

is the population size in total biomass (Owen-Smith 2002).

The effect of the herbivores on landscape heterogeneity depends on the interaction between the pre-existing spatial pattern of the vegetation and the spatial pattern of herbivory (Bakker *et al.* 1984; Adler *et al.* 2001), which is determined by the distribution of the herbivores. Herbivore distribution itself is determined by various factors (Coughenour 1991; Bailey *et al.* 1996; Hobbs 1996, 1999; Adler *et al.* 2001), but in our model, we confine ourselves to forage as one of the prime determinants. Both forage availability and forage quality play an important role in herbivore distribution: selective foraging occurs in preferred areas. According to optimal foraging theory, animals forage in a way that maximises the immediate rate of energy gain (Stephens & Krebs 1986). Therefore, the instantaneous energy gain through consuming resources in a cell is taken as measure for the attractiveness of a cell for herbivores. This attractiveness does not only depend on the instantaneous intake rate of food, but also on the digestible energy content of the food (Prins & Olff 1998; Owen-Smith 2002; Drescher *et al.* 2006). We calculate the instantaneous intake rate (I) for both grazers and browsers by means of an asymptotic type II functional response:

$$I = \frac{i_{max}\,F}{g_{\frac{1}{2}} + F} \tag{3.9}$$

where i_{max} is the maximum food intake rate at high food abundance, F is the food availability and $g_{\frac{1}{2}}$ is the food availability at which I reaches half of its maximum (Owen-Smith 2002). Only the amount of browseable woody biomass within the physical reach of the browsers is considered as available browse, while the total amount of herbaceous biomass is assumed available for the grazers. The instantaneous rate of energy gain from consuming forage in a cell (E) can be calculated by adding a reduction term for the digestibility of the forage material (Owen-Smith 2002):

$$E = \frac{i_{max}\,F}{g_{\frac{1}{2}} + F}(1-q)^F \tag{3.10}$$

where q is the reduction term of forage digestibility with increasing standing biomass. Digestibility of grass biomass has been reported to be negatively correlated with standing biomass (Prins & Olff 1998; Anderson *et al.* 2007), while the digestibility of browseable material remains constant (Woolnough & Du Toit 2001).

Self-facilitation

In our model, the herbivores interact with the vegetation by influencing the vegetation characteristics while foraging (standing biomass, forage quality or vertical zonation), which, in turn, determine the attractiveness of a cell to the herbivores. The mechanism for self-facilitation through grazing is the decreasing nutritive quality of grass vegetation with increasing standing biomass as in Eq. 3.10. Hence, grazers increase the attractiveness of grazed cells by decreasing the standing crop and simultaneously increasing the nutritive quality of vegetation. Grazed cells are consequently visited repeatedly as long as regrowth of the grass is faster than the time within which grazers return. In contrast to grazers, browsers do not experience a decline in forage quality with increasing standing woody biomass. Browsers select cells with the highest amount of browseable

biomass that is within their reach because of the vertical structure of the woody vegetation. Although browsing results in a decrease of the amount of reachable forage in the short term, the amount of accessible browse in the long term remains high relative to a situation without browsers (Fig. 3.1). Hence, browsers are able to facilitate themselves by increasing the amount of available (i.e., reachable) forage by keeping the trees short and stimulating the regeneration and regrowth of woody vegetation. These abovementioned results show that the herbivores exhibit self-facilitation, either by increasing the nutritional quality of regrowth following defoliation, or by inducing changes in resource allocation and plant architecture (i.e., vertical zonation of browseable biomass). Hence, foraging in a cell increases the attractiveness of the cell and thereby the chance that the cell will be selected in the near future.

Spatial dependency of foraging

The distribution of the herbivores does not only depend on the attractiveness of single cells, it may also result from decisions made by the animals at larger spatial scales (Senft *et al.* 1987; Bailey *et al.* 1996). Herbivores are thought to select the landscape unit richest in resources, then the most productive locations within this landscape unit, and so on, down to the most palatable species within a feeding station (Bailey *et al.* 1996). Foraging decisions at broad spatial scales thus can constrain choices at smaller scales (Bailey *et al.* 1996). We therefore calculate the attractiveness of a cell as a weighted average of the attractiveness of all cells in its vicinity using inverse distance weighting:

$$w = dist^{wf} \tag{3.11}$$

where w is the weighting factor of a cell and wf is the weighting exponent of a cell with distance *dist* to the cell of focus. In this way, the attractiveness of large-scale landscape units influences the attractiveness of a single cell within this unit.

Herbivory at a certain location also affects the vegetation in neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza *et al.* 2006). While foraging in a cell, the herbivores are therefore modelled to also remove a constant fraction (*adj*) of λ from the adjacent cells.

Model analyses

Following Murwira & Skidmore (2005), we used variograms to quantify the spatial heterogeneity of the simulated landscapes by quantifying the heterogeneity and dominant scale of these landscapes, where dominant scale is a measure for the average vegetation patch size. A variogram expresses the degree of spatial variation of a regionalised variable, here grass and woody biomass, as a function of distance:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_{i+h}) \right]^2 \tag{3.12}$$

where $\gamma(h)$ is the semivariance at lag h (i.e., the beeline distance between sample locations x_i and x_{i+h}), $N(h)$ is the number of observation pairs separated by h, $z(x_i)$ is the value of the regionalised variable at location x_i, and $z(x_{i+h})$ is the value of the regionalised variable at distance h from x_i (Murwira & Skidmore 2005). To calculate the empirical variograms and to fit an exponential variogram model through the data (Fig.

3.2), we used the statistical package R (R Development Core Team 2009) with the gstat library for geo-statistical analyses (Pebesma 2004, 2007). The two main structural parameters of the variogram, the sill and the range (Fig. 3.2) are calculated and used to measure respectively the heterogeneity and dominant scale of vegetation.
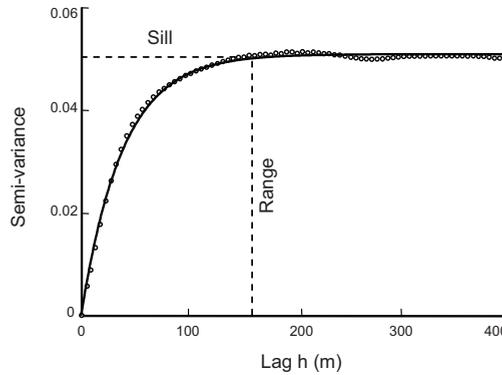

Figure 3.2: The use of variograms to expresses the degree of spatial variation of grass and woody biomass as a function of lag distance *h*. The sill of the variogram (i.e., the semi-variance where the variogram levels off) is used to measure the heterogeneity of the simulated landscapes, while the range (i.e., the lag-distance where the variogram levels off) is used as a measure for the dominant scale of the vegetation patterns.

Simulations

We simulated model scenarios with variation in parameter values and initial landscapes. We started with simulations where both self-facilitation and spatially explicit foraging were systematically included in the model to understand their independent effects on spatial pattern formation as well as their interactive effects. We then performed simulations in which we varied the densities of the browsers and grazers. All of these simulations were performed on initial landscapes that had random amounts of grass and tree biomass in each cell drawn from a uniform distribution.

Finally, we performed a series of simulations in which we incorporated both different levels of heterogeneity as well as different dominant scales of the initial landscape. Different levels of heterogeneity in the initial landscapes were obtained by changing the minimum and maximum values between which random values for grass and woody biomass were drawn. Different dominant scales of the initial landscapes was introduced by grouping cells together and assigning them the same random value for grass or woody biomass.

Results

If we analyse the model without herbivores, the resultant standing biomass of trees and grasses in each grid cell is only determined by the amount of infiltrated water and the soil characteristics, with dynamics as outlined by Van Langevelde *et al.* (2003). Since we kept the amount of infiltrated water and soil characteristics equal for all cells and constant during the simulations, every cell is identical to the others resulting in homogeneous vegetation without patterning, regardless of the initial landscape conditions. The tree
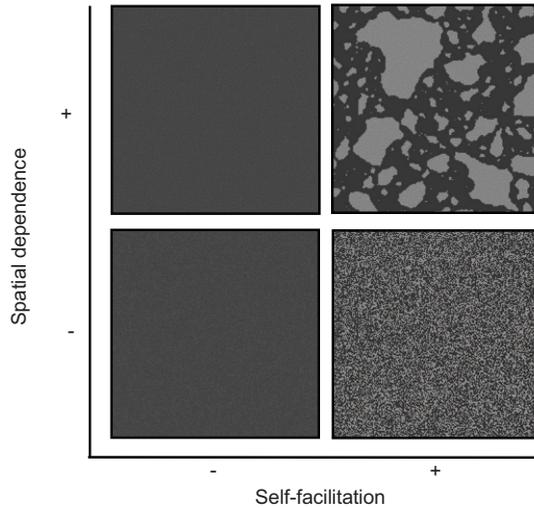
Figure 3.3: Vegetation patterns after 500 year of simulation in relation to the two driving mechanisms: spatial dependency of foraging and self-facilitation, where − means that the assumption is not included in the model, whereas + means that the assumption is included in the model. Both assumptions need to be simultaneously included in order to induce vegetation patterning. The grey tone represents the amount of biomass, with dark grey expressing a high biomass, and light grey a low biomass. The landscapes confine 200 x 200 cells of 5 x 5 m each.

layer then consists exclusively of trees in the highest cohorts, for there are no disturbances that prevent the trees from growing tall (Fig. 3.1).

Conditions for herbivores to induce vegetation patterning

If we exclude both self-facilitation and spatial dependency of foraging from the model (i.e., grazing does not increase the nutritional quality of grass vegetation, the browsers can access the entire tree canopy, and the selection of a cell is not influenced by its neighbourhood), the herbivores create a landscape with only fine-scale cell-to-cell variation, but without broad-scale vegetation patterns (Fig. 3.3). The fine-scale heterogeneity in vegetation results from a reduction of forage material in the cells where the herbivores fed relative to the surrounding matrix. In this scenario, the herbivores select only the cells with the highest standing biomass, irrespective of the cell's location. Foraging decreases the attractiveness of these cells and thus the chance that they are selected in the near future. When including self-facilitation, but excluding spatial dependency of foraging, the resultant landscape shows only fine-scale patterning due to selective foraging in preferred cells (Fig. 3.3). Due to self-facilitation, selected cells are frequently revisited, but the selection of sites is not influenced by the spatial arrangement of the sites. When spatial dependency of foraging is included, but self-facilitation excluded from the model, there is no reason for the herbivores to frequently revisit a site and hence they create virtually homogeneous vegetation with only slight cell-to-cell heterogeneity (Fig. 3.3). Only when both key assumptions are simultaneously included, the herbivores are able to create stable, broad-scale vegetation patterns (Fig. 3.3). The herbivores then frequently revisit sites due to self-facilitation, where larger patches are preferred above smaller ones

due to spatial dependence of foraging.

To understand the separate effects of the components of self-facilitation and spatial dependency of foraging on vegetation patterning, we analyse the model, varying the parameters wf, adj, q and $bhmax$, while calculating the dominant scale and heterogeneity of the resultant landscapes. An increase of the weighting of surrounding cells in the assessment of a cell's attractiveness (wf) or the amount of forage consumed in adjacent cells (adj) results in an increase of the dominant scale of the vegetation patterns, but the heterogeneity remains relatively unaffected (Fig. 3.4a-b). Increasing the decrease of forage quality with increasing grass biomass (q) increases the heterogeneity and dominant scale of the resultant vegetation (Fig. 3.4c). This means that when grazers are more able to increase the forage quality while foraging, the grazed patches become larger, and the spatial heterogeneity becomes higher. The dominant scale of the vegetation increases with increasing q since grazing increasingly facilitates the quality of forage material, also in adjacent cells, and this in turn increases the attractiveness of the selected cell, but also the attractiveness of the cells in its near surroundings. Through altering the maximum height that the browsers can reach ($bhmax$), we see that the browsers only induce spatial vegetation patterning when they are able to access a large part of the tree canopy, but not entirely (Fig. 3.4d). Only then are browsers able to facilitate themselves, for they are able to suppress the woody vegetation, in which case there would be more reachable forage compared to an unbrowsed situation (Fig. 3.1). When the browsers can only access a small proportion of the tree canopy, their ability to suppress the woody vegetation is limited, and hence self-facilitation is not important for them. When the browsers can access the entire tree canopy, there is no self-facilitation and hence no vegetation patterning, for it is not necessary to alter the plant architecture in order to increase the amount of reachable browse.

Changing herbivore density

In the previous section, we showed that both key assumptions have to be included simultaneously in the model to induce spatial vegetation patterning. We now analyse the behaviour of the model while including both mechanisms simultaneously and varying herbivore densities. At low grazing pressure, the grazers create small grazed patches (Fig. 3.5a). With increasing grazing pressure, the grazed patches become larger, until eventually the grazers exploit the entire landscape and create only fine-scale cell-to-cell heterogeneity, as explained above. As a result, the heterogeneity and dominant scale of the vegetation show a hump-shaped response to increasing grazing pressure (Fig. 3.6a). The same holds for the browsers: at low browser density, the browsers suppress the woody vegetation in the cells that they select to forage, while the trees in unutilised cells are able to grow to full size, resulting in browsed patches of small trees surrounded by large trees. With increasing browser density, the browsed patches grow in size until the browsers utilise almost the entire woody vegetation, with only scattered areas of unbrowsed vegetation (Fig. 3.5b). When browser density then increases even more, they are able to suppress the entire woody vegetation, creating spatially homogeneous vegetation at a broad scale, with only fine-scale differences in biomass removal from selected and adjacent cells. The dominant scale and heterogeneity of the woody vegetation therefore also show a hump-shaped response to browser density (Fig. 3.6b).
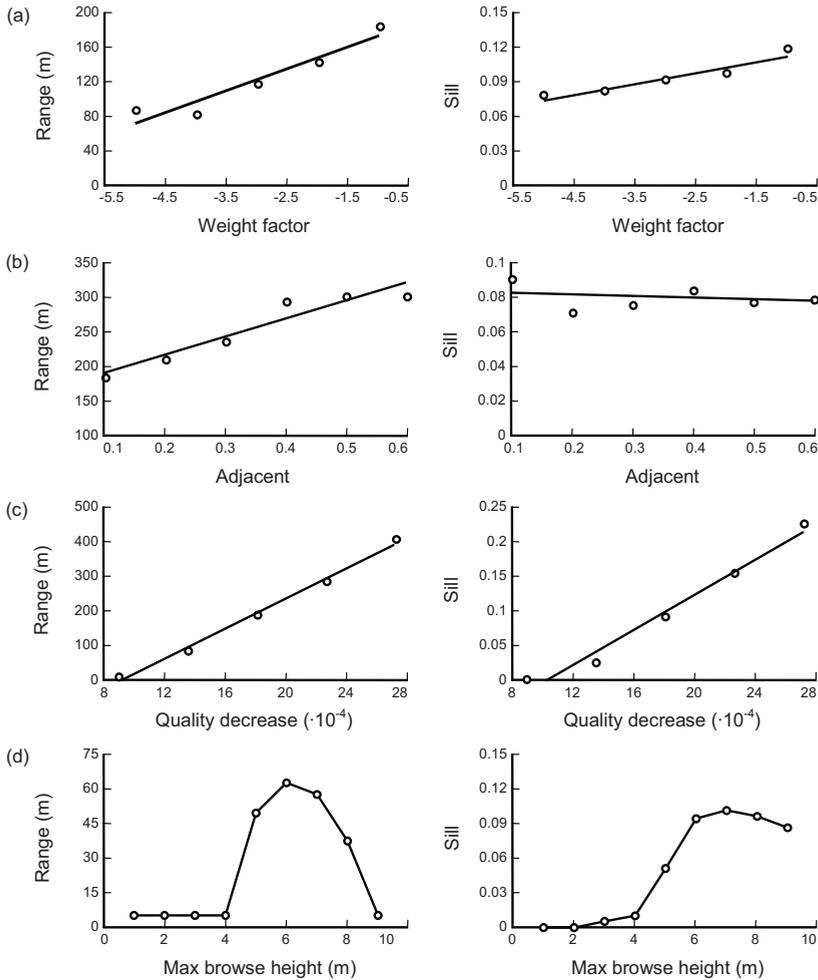
Figure 3.4: The range and sill of the variograms as measure for the dominant scale and heterogeneity of the vegetation patterns (Fig. 3.2) while varying parameter settings for spatial dependency of foraging: (a) the weighting exponent of neighbouring cells (wf) and (b) the fraction of λ that is removed from adjacent cells (adj), and self-facilitation: (c) the decrease of nutritional quality with increasing grass biomass (q) and (d) the height till which the browsers can reach ($bhmax$). All parameter values as in Table 3.1 except for the parameter under change.

Interactions with pre-existing vegetation patterns

Analysis of the model with different initial landscape configurations shows that both the heterogeneity of the initial vegetation as well as the dominant scale of the pre-existing vegetation patterns influence the vegetation patterns as produced by the herbivores (Fig. 3.7). The dominant scale of the resultant vegetation patterns increases when the dominant scale of the initial vegetation increases (Fig. 3.7a), meaning that the level of adherence of the herbivores to forage in pre-existing patches increases when these pre-existing
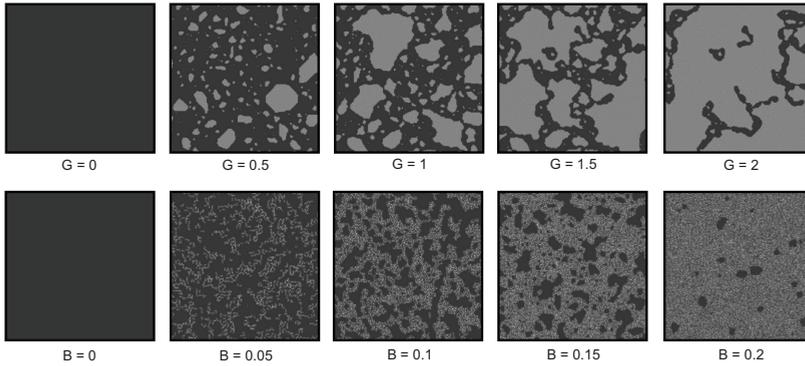
Figure 3.5: Stable patterns in grass (a) and woody (b) vegetation after 500 yr of simulation as a function of grazer (*G*) and browser (*B*) density (g m^{-2}), respectively. The grey tones represent the amount of grass or woody biomass, with dark grey expressing a high biomass, and light grey a low biomass. Each landscape confines 200 x 200 cells of 5 x 5 m each.

patches increase in size. With increasing heterogeneity of the initial landscape, the dominant scale of the resultant vegetation decreases (Fig. 3.7b).

Discussion

In this paper, we address the question whether and through which mechanisms herbivores can induce spatial patterning in savanna vegetation, and how the role of herbivory as a determinant of vegetation patterning changes with variation in herbivore density
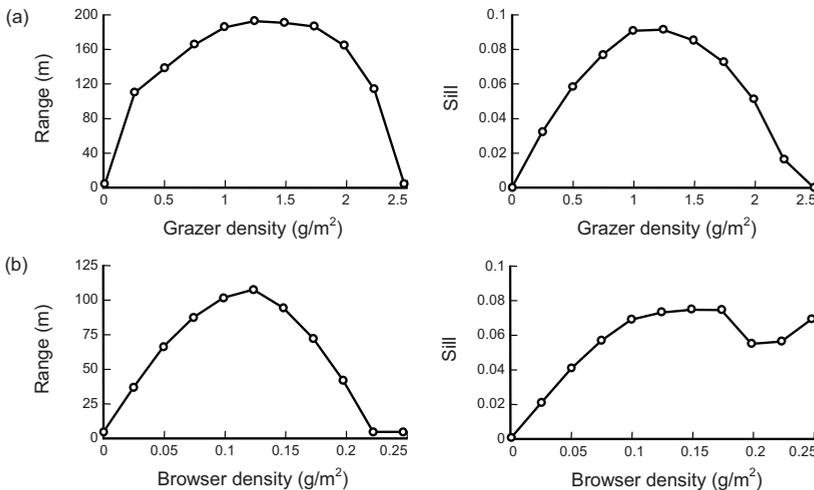
Figure 3.6: The dominant scale (i.e., range, Fig. 3.2) and heterogeneity (i.e., sill) of the vegetation in relation to (a) grazer density and (b) browser density.
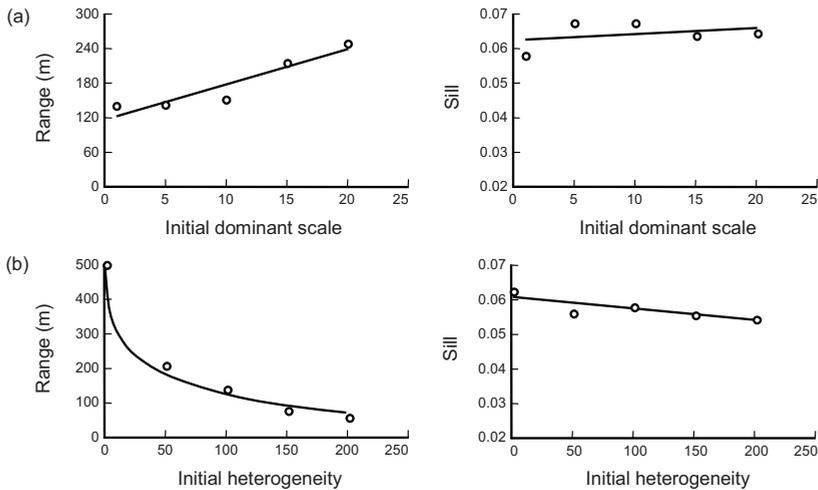
Figure 3.7: The dominant scale (i.e., range, Fig. 3.2) and heterogeneity (i.e., sill) of the simulated vegetation in relation to (a) the dominant scale of the initial landscape (ds, where ds by ds cells are all assigned the same random value of grass biomass), and (b) the heterogeneity of the initial landscape (i: computed as the interval $280 \pm i$ out of which random values are drawn to be assigned to each cell).

and the pre-existing pattern of vegetation. To answer these questions, we developed a spatially explicit simulation model, including growth of grasses and trees, vertical zonation of browseable biomass, and spatially explicit foraging by grazers and browsers. The trends produced by the model show that the formation of spatial vegetation patterns in savannas due to herbivory critically depends on the interaction between two mechanisms, namely self-facilitation by the herbivores and spatial dependency of foraging. This means that (1) there has to be a reason for herbivores to revisit a site, e.g., through an increased availability or quality of forage, and (2) foraging at a site should relate to vegetation at larger spatial scales.

Self-facilitation can emerge from increasing the nutritional quality of vegetation or increasing the forage availability while foraging. In our model, the first case applies to the grazers, while the latter one is applicable to the browsers. Adler *et al.* (2001) argue that feedbacks between grazing and plant quality may be important sources of spatial patterning since they promote the continued use of previously grazed patches. These feedbacks include increased nutritional content of the forage material, a reduction in senescent material and maintenance of leaves in an early phenological state (Coppock *et al.* 1983; McNaughton 1984; Jefferies *et al.* 1994; Hobbs 1999; Anderson *et al.* 2007). The vegetation patterns of grass biomass as produced by our model resemble the "grazing lawn" phenomenon where ungulate grazers are able to maintain permanent grazing lawns through a positive feedback loop (grazing-regrowth-regrazing) that generates enhanced productivity in a short sward (McNaughton 1984; Anderson *et al.* 2007). The model output also resembles the vegetation patterns that Bakker *et al.* (1984) and Cid & Brizuela (1998) found as result of grazing by sheep and Aberdeen Angus steer, respectively, on initially uniform paddocks. They showed that the sheep and cattle revisited some sites within the paddocks more often while neglecting other sites, resulting in a

mosaic of heavily utilised and lightly utilised patches, as do our simulated grazers.

While grazing enhances the quality of forage material in our model, browsing increases the amount of browse within reach of the herbivores. High browsing pressure can prevent the establishment of woody seedlings and retard the growth of shrubs, suppressing their recruitment into the mature stage (Pellew 1983; Prins & Van der Jeugd 1993; Roques *et al.* 2001; Augustine & McNaughton 2004; Fornara & Toit 2007). In this way, patches are created where trees are being suppressed by the browsers while in other areas trees can escape this suppression and reach a "size refuge" when the browsers are not able to suppress the entire woody vegetation (Fornara & Toit 2007). Analogous to the grazing lawns, Fornara & Toit (2007) call these browsed patches "browsing lawns" since chronic browsing by ungulates can maintain trees in a suppressed and hedged state, thereby inducing changes in resource allocation and plant architecture and hence making more food available to browsers.

Although self-facilitation is a prerequisite for vegetation patterning to occur in our model, we claim that self-facilitation alone is not sufficient to induce spatial patterning in savanna vegetation through herbivory. The interaction of self-facilitation with spatial dependency of foraging is found to be crucial to induce patterning. We modelled spatial dependency of foraging by including the attractiveness of a cell's environment in the assessment of the attractiveness of the particular cell, and by foraging in cells adjacent to selected cells. The first case can be interpreted as hierarchical foraging decisions (Senft *et al.* 1987; Bailey *et al.* 1996), where herbivores make decisions at different spatial-temporal scales and where large-scale decisions influence decisions at smaller scales. The herbivore pressure at a certain location also results in consuming the vegetation at neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza *et al.* 2006). This effect of foraging at neighbouring locations is small when the central location attracts few herbivores, and it decreases with increasing distance from the central location to which the herbivores are attracted.

Analysis of our model shows that the heterogeneity and dominant scale of the resultant vegetation patterns is highest at intermediate herbivore densities. With higher herbivore densities, the herbivores are forced to be less selective, and hence the level of heterogeneity of the vegetation decreases. These findings are consistent with the predictions from Adler *et al.* (2001) that the heterogeneity of vegetation decreases when the removal of plant tissue through herbivory is distributed spatially more homogeneously. Our model also shows that the pre-existing pattern of vegetation increasingly influences vegetation patterning through herbivory when the heterogeneity of the initial landscape increases. Adler *et al.* (2001) postulate that when grazing is a dependent function of the pre-existing vegetation pattern (termed "selective grazing" in their paper), then patterns emerge only if grazing positively influences the resource levels of grazed patches (i.e., self-facilitation), and otherwise patterns will disappear. We also generated this hypothesis because only through the inclusion of self-facilitation spatial vegetation patterns could be produced. Additionally, we showed that the influence of the pre-existing vegetation in determining vegetation patterning through herbivory decreases when the initial heterogeneity and dominant scale of the initial vegetation is smaller. With initially low vegetation heterogeneity, the herbivores are able to shape the vegetation, but they adhere more to the pre-existing vegetation patterns when the initial vegetation heterogeneity increases. Although the heterogeneity and dominant scale of the initial landscapes do

influence the dominant scale of the resultant landscapes, they do not severely influence the heterogeneity of the resultant landscapes, suggesting the heterogeneity of the resultant landscapes is more a property of the herbivores than it is influenced by the initial landscape configuration.

Contrary to our finding that self-facilitation is a necessary mechanism to induce spatial patterning in savanna vegetation, the positive effect of repeated grazing on forage quality can decline in the long term, when grazing remains intensive and leads to a change in plant species composition to less palatable species (Coppock *et al.* 1983). As we did not take plant species composition into account, our model could not reproduce this reversing effect. Furthermore, overgrazing can lead to an increase of woody vegetation at the cost of palatable grasses, often referred to as "bush encroachment" (Roques *et al.* 2001). In our model, the simulated grazers and browsers forage exclusively on grass and woody vegetation, respectively. Hence, the grazers do not directly influence the woody vegetation, but only indirectly through removing grass biomass in selected cells, thereby decreasing the competitive ability of the grass vegetation and stimulating the growth of trees. Likewise, the browsers do not directly influence the grass vegetation, but only indirectly through influencing resource competition between grasses and trees. Hence, grazing at a site increases the competitive advantage of trees and therefore the biomass of the woody vegetation, what corresponds to the bush encroachment phenomenon that is often observed. However, the increased growth of woody vegetation attracts more browsers which, when the browser density is high enough, can suppress the woody vegetation as shown above. This might diminish the risk of bush encroachment. Because we did not model individual species but only plant functional groups, the negative effect of an increased biomass of the woody vegetation on grass species composition and palatability could not be reproduced. Nevertheless, the reversing effects of herbivory on forage characteristics could reduce or contradict the mechanism of self-facilitation that we postulate above.

Recently, a body of theory has emerged emphasizing a scale-dependent feedback between localized facilitation and large-scale inhibition of plant growth driving patterning and self-organisation in vegetation (Klausmeier 1999; Rietkerk *et al.* 2002a, 2004; Kéfi *et al.* 2007; Scanlon *et al.* 2007; Van Wesenbeeck *et al.* 2008). In arid systems, for example, infiltration of water is locally enhanced by plant presence, while on landscape scales competition for water between plants is the dominant process explaining observed vegetation patterns (Rietkerk *et al.* 2002a; Van Wesenbeeck *et al.* 2008). In this paper, we posit an alternative mechanism behind spatial patterning in savanna vegetation, namely the interaction between spatial dependent selectivity of herbivores and forage enhancement due to self-facilitation. We think that this mechanism is more appropriate in semi-arid and mesic savannas characterized by a continuous vegetation cover, where herbivores can induce vegetation patterning through localized reduction of vegetation biomass and/or alteration of plant architecture. Hence, we hypothesize that the role of herbivores in pattern formation is of greater significance when the moisture availability increases, enabling herbivores to forage selectively while enhancing forage quality and regrowth. With increasing water availability, the vegetation can supply the herbivores with more forage, enabling a higher herbivore density that still induces vegetation patterning (i.e., Fig. 3.6 stretches out to the right). At very high levels of water availability, the vegetation is completely dominated by trees (Van Langevelde *et al.* 2003; Sankaran *et al.* 2005).

In this paper, we showed that herbivores at intermediate densities can induce spatial patterning in savanna vegetation through the interactions between self-facilitation and spatial dependency of foraging, with the type of pattern being influence by the heterogeneity and dominant scale of the pre-existing vegetation. The findings presented here, and critical experimentation of their ecological validity, increase our understanding of heterogeneity and patterning in savanna vegetation, and the role of plant-herbivore interactions therein.

HJ de Knegt, Y Pretorius, F van Langevelde, WF de Boer, G Gort, AK Skidmore, R Slotow, S Henley, A Delsink, CC Grant & HHT Prins

4

Visited sites revisited - site fidelity in African elephants

Various reasons exist why animals revisit previously visited sites, ranging from natal philopatry and spatial neophobia, to positive plant-herbivore feedbacks. Here, we focus on the patterns of site revisitation by African elephants in Kruger National Park, South Africa, and specifically specifically focus on the influence of their two main resources, vegetation and water, on their patterns of site revisitation. Because surface water availability varies seasonally, and because vegetation growth is dependent on seasonal rainfall patterns, we analyze the patterns of site revisitation in relation to these resources taking into account seasonality in rainfall. We show that elephants do not avoid previously utilized areas but seem to exhibit the tendency to return to sites already visited above what can be expected from random movements alone. Furthermore, the patterns of site fidelity were not solely determined by the preference for certain sites independent of past experience, as some sites were often visited but not much revisited and others not much visited but often revisited. The elephants were more likely to be site-faithful when surface water became scarce (dry season) and in areas close to water. Overall, tree cover was negatively correlated to the rate of site revisitation by elephants. However, female elephants revisited sites close to water and with high tree cover more often, probably because these areas provide not only water, but also shelter and abundant forage that is of high quality. Although we did not find strong overall differences between male and female elephants, the female elephants seemingly timed revisits to specific sites taking into account the environmental (tree cover and distance to nearest water source) and climatic conditions (rainfall). This might be due to the more stringent requirements regarding the quality and accessibility of forage regarding the female elephants and the young individuals within family herds, which we hypothesize to increase the incentive to consume the regrowth of vegetation previously been utilized. We conclude that familiarity with specific sites influences the movements and habitat selection by African elephants, patterns of which are mediated by seasonally varying abundance of surface water and growth of vegetation.

Introduction

Studies of habitat selection, a central topic in ecology, often relate the geographical distribution of species to characteristics of their environment (Araújo & Guisan 2006; Hirzel & Le Lay 2008). Such analyses typically consider habitat selection as being determined by exogenous predictors (i.e., environmental characteristics), ignoring the interactions of consumers with their resources and the importance of an individual being familiar with an area due to past use (Guisan *et al.* 2006; Wolf *et al.* 2009). However, many species have the ability to remember previously visited sites and tend to revisit them periodically (Börger *et al.* 2008). This site fidelity is well known in migratory species that exhibit breeding-site fidelity or species exhibiting natal philopatry (Greenwood & Harvey 1982; Switzer 1993; Davis & Stamps 2004). Moreover, herbivorous species might also return to previously visited sites because of plant-herbivore feedbacks (Gordon & Lindsay 1990; De Knegt *et al.* 2008).

Namely, while foraging causes resource depression, so that foragers move away and avoid this site shortly thereafter (Charnov 1976; Ohashi & Thomson 2005), different considerations may emerge over longer time scales. As time elapses, food resources replenish, so that revisiting these food resources may become profitable (Gill 1988; Possingham 1989; Williams & Thomson 1998; Ohashi & Thomson 2005). Additionally, herbivory may cause plant responses that are advantageous to the herbivores, through improvement in the quality, biomass or the density of the foliage on offer (McNaughton 1983; Gordon & Lindsay 1990; Nunez-Farfan *et al.* 2007; De Knegt *et al.* 2008; Kohi *et al.* 2010). This can induce a positive feedback between plant and herbivore, leading to the repeated revisitation of visited sites (Makhabu *et al.* 2006; De Knegt *et al.* 2008; Kerley *et al.* 2008). The renewal of plant material with successive exploitation by foragers is characteristic of many herbivore-plant systems (Prins *et al.* 1980). In such systems, the rate of resource renewal is predicted to influence the foragers' decisions about when to revisit foraging sites, so that foragers benefit by returning more often to highly profitable foraging areas than to less profitable ones (Watts 1998).

These decisions depend on the presence of spatial memory ("what-and-where") or even episodic-like memory ("what-where-and-when") (Clayton & Dickinson 1998; Crystal 2006). Memory enhances the efficiency with which animals can exploit their resources; it makes it easier to return to places and things that are useful, and to avoid those that may be dangerous or costly (Collett 2009). It has been demonstrated that birds (Prins *et al.* 1980; Gill 1988; Clayton & Dickinson 1998; Henderson *et al.* 2006), insects (Williams & Thomson 1998; Cartar 2004; Boisvert & Sherry 2006; Skorupski & Chittka 2006; Ohashi *et al.* 2007; Van Nouhuys & Kaartinen 2008) and small mammals (Eacott *et al.* 2005; Babb & Crystal 2006) can time revisits to specific sites based on the rates and timing of resource renewal. Albeit only few studies have investigated the patterns of site revisitation by large free-ranging mammalian herbivores (i.e., Watts 1998; Wolf *et al.* 2009), these studies have shown that spatial familiarity may be very important in determining the movements of large herbivores.

In this paper, we study the patterns of site revisitation by the largest terrestrial animal species, the African elephant (*Loxodonta africana*), in Kruger National Park (KNP) in South Africa. We expect elephants to revisit sites frequently because of a twofold reason. First, they are regarded as an important factor in modifying the savanna landscape, because their very large body size enables them to restructure the vegetation, forming "browsing lawns", i.e., areas with a reduced height of the woody vegetation and an in-

creased quality of forage material (Jachmann & Bell 1985; Smallie & O'Connor 2000; Fornara & Toit 2007; Erwin 2008; Kerley *et al.* 2008). This leads to a larger portion of the canopy being accessible to them, and generally a higher nutritional value of regrowth shoots, increasing the probability of revisiting a previously browsed plant (Fornara & Toit 2007; De Knegt *et al.* 2008; Skarpe & Hester 2008). Second, they have long-term spatial memory, enabling them to anticipate to the renewal of resources distributed in space (McComb *et al.* 2001; Van Aarde *et al.* 2008; Van Langevelde & Prins 2008). Our aim is to assess the frequency with which sites are being revisited by elephants, and to determine the environmental factors that influence site fidelity by this megaherbivore.

As the opportunity for plant regrowth is largely determined by environmental conditions, particularly by the extent and timing of moisture availability (Begon *et al.* 1996; Hobbs 1996), the frequency of site revisitation by elephants is expected to be positively correlated to the amount of rainfall available for regrowth. However, rainfall influences the amount of surface water availability, a key resource determining elephant distribution, especially in periods when seasonal water sources dry up (Chamaille-Jammes *et al.* 2007b; Harris *et al.* 2008; Van Aarde *et al.* 2008). Hence, elephants tend to concentrate their foraging activities in relatively small ranges close to water, especially during the dry season (Smit *et al.* 2007c; Van Aarde *et al.* 2008; Loarie *et al.* 2009a). Thus, the concentration of elephants in smaller areas during the dry season may lead to proportionally more revisits during dry periods.

Furthermore, foraging in groups seems to be an efficient strategy to exploit renewing resources, as individuals in groups are less likely to revisit sites that have already been exploited recently by others (Beauchamp & Ruxton 2005). In African elephants, females live in matrilineal family units, generally spending their entire lives in tightly knit social groups while living in a specific area, whereas male elephants are generally solitary or in smaller bachelor herds, travelling longer distances over a more extensive area (McComb *et al.* 2001; Wittemyer & Getz 2007; Van Aarde *et al.* 2008). Thus, male and female elephants might exhibit different patterns of site revisitation, where female elephants are expected to revisit sites more often due to their smaller home ranges and foraging in larger herds.

We test the hypotheses that elephants revisit specific sites (1) more often than can be expected based on chance alone, (2) close to water more often than sites far from water, (3) with high tree cover more often than areas with low tree cover, (4) more often during dry periods, and (5) female elephants revisit sites more often than male elephants.

Methods

Study site and species

KNP is South Africa's largest nature reserve, covering roughly 19000 km^2 and harbouring around 14000 elephants. Six perennial rivers cross the park from west to east, while several ephemeral rivers only contain water during the wet season (Smit *et al.* 2007c). Furthermore, the park contains around 300 water points (pans and artificial boreholes). KNP receives between 400 mm and 940 mm rain annually, in respectively the northern and southern parts of the park, with a rainy season from December to March. From November 2005 till October 2008, 43 elephants (18 males and 25 females) were followed using global positioning system (GPS) collars (Hawk105 collars, Africa Wildlife Tracking cc., South Africa), recording their locations at hourly intervals. This resulted in 242539 recorded locations, with a positional precision of ≤ 27.8 m in 95% of the records.

Site re-visitation

For an elephant to *re*-visit a site, it first must have left the site (Switzer 1993). Hence, we used two distance thresholds to determine whether a site has been revisited: (1) the elephant being followed had left a particular site if it moved further than 1 km from the focal site, and (2) the focal site was considered to be revisited if the elephant subsequently came sufficiently close again, for which we used a 100 m distance threshold. We chose these distance thresholds to avoid immediate returns when both thresholds were set at the same distance, and to have a relatively high certainty that the elephant was indeed back at a previously visited site.

Both events, i.e., visit and revisit, are thus closely separated in space (max 100 m), but possibly far apart in time, yet constrained by the time frame over which the GPS locations were recorded (maximally ca. 3 years). One could argue that all visited locations in the study area would eventually be revisited, when the elephants are given enough time to walk around. Hence, the main question is not *whether* a site will be revisited or not, but *how long* it takes before a site is being revisited, which we refer to as the *revisitation interval*. For each location visited by an elephant, we thus assessed whether this elephant did revisit the site, while recording the time (in number of days) that had elapsed between visit and revisit.

Survival analysis

We analyzed the patterns of site revisitation using survival analysis, which originally refers to the time to death (i.e., survival time). Survival analysis focuses on the time between two events, namely the time between visit and revisit in our study. If each site is revisited, many methods of analysis would be applicable, since the distribution of revisitation intervals would then be known (Bradburn *et al.* 2003b). However, sites that are not revisited before the end of the observation period (right-censored data) leads to partial information regarding the distribution of revisitation intervals. Survival analysis offers methods to analyse such data, describing the distribution of time-to-event data while taking into account censoring, and estimating the effect of covariates on the survival time (Bradburn *et al.* 2003a; Clark *et al.* 2003; Kleinbaum & Klein 2005).

The distribution of survival times is usually defined in terms of the *survival function*, $S(t)$, or the *hazard function*, $h(t)$. The survival function describes the probability that an event did not occur before time t, whereas the hazard function expresses the event rate at time t, given that an event has not occurred until time t. We estimated the survival function for the revisitation intervals nonparametrically using the Kaplan-Meier method (Kleinbaum & Klein 2005). To assess the influence of covariates on the survival time, we used the Cox proportional hazards (PH) procedure (Cox 1972). The Cox PH regression model expresses the survival time data by means of a baseline hazard function plus the influence of covariates:

$$h(t) = h_0(t) \exp\left(\sum \beta_i x_i\right) \tag{4.1}$$

where the hazard function $h(t)$ is dependent on a set of p covariates x_i, whose impact is measured by the size of the coefficients β_i (Bradburn *et al.* 2003a). The term h_0 is the baseline hazard shared by all records, i.e., the hazard if all coefficients are equal to zero. The influence of the covariates on the hazard rate is thus modelled as a multiplicative effect of $\exp\left(\sum \beta_i x_i\right)$ on the baseline hazard $h_0(t)$, with values above 1 indicating that the hazard rate increases (resulting in shorter survival times); below 1 the hazard rate decreases (Bradburn *et al.* 2003b; Kleinbaum & Klein 2005).

Dealing with serial correlation and observation length

Since sequential locations of GPS-tagged individuals may be temporally dependent (Gutz-willer & Riffel 2007), we only used locations that were separated six hours apart, because serial correlation in the dichotomous event of revisitation or censoring then vanished. We used all data at hourly intervals to assess whether each site was revisited or not.

Furthermore, because the amount of time that the elephants were monitored was not equal for all elephants, we checked whether the observation length influenced the robustness of our analyses using simulated data. Thereto, we simulated movement paths with equal mathematical properties, but differing in path length: 30,000 vs. 60,000 locations per path. We assessed the influence of path length on the pattern of site revisitation using Cox PH regression by analysing whether the coefficient significantly differed from the expected value of 0 in case path length does not influence the analyses. We analysed this for 100 randomizations of the movement paths, and concluded that path length did not influence our analyses ($P = 0.798$, one-sample t-test, $n = 100$, $t = 0.256$), which is in line with Wolf *et al.* (2009), who observed no relationship between the amount of time an individual was monitored and the proportion of locations that was revisited.

Comparing to null models

Because site revisitation by the elephants could be due to chance alone, we compared the observed patterns of site revisitation to random alternatives. We analyzed whether the observed pattern of site revisitation differed from that of randomly moving individuals, for which we randomized the observed movement paths following the bootstrap procedure as described by Turchin (1998) and De Knegt *et al.* (2007). Similar to the procedure described above, we tested whether the coefficient of a Cox PH regression differed significantly from the expected value of 0.

To test whether the patterns of site revisitation reflected the overall preference for certain habitats or whether additional factors are important, we used an approach similar to the problem of identifying spatial patterns in a disease rate. This is often done through estimating the local density of an event (in our case a site being revisited), taking into account the local density of the population that is at risk (in our study the overall preference of the elephants for certain habitats reflected by the local elephant density) (Pickle 2002; Rushton 2003; Rushton *et al.* 2004; Wallar 2009). We estimated the local density of all sites, as well as only those that were revisited, using a two-dimensional Gaussian kernel with a bandwidth of 1 km. Dividing the kernel density estimate of the revisited sites by that of all sites yielded the relative local revisitation rate, expressed as the proportion of the visited sites that is being revisited. We then classified both the overall density and the relative revisitation density into two binary classes: low (given the value 0) and high (given the value 1), with the median value for both density functions as the break point. We analysed the patterns of site revisitation using Cox PH regression with both binary variables as covariates.

Relating site revisitation to covariates

To test our hypotheses, we related the patterns of site revisitation by the elephants to several covariates. For each visited location, we calculated its Euclidean distance to the nearest source of surface water, from both natural (rivers) and artificial (water points, dams) sources. Tree cover associated to each visited site was estimated using field data, Landsat and JERS-1 (radar) imagery, as described by Bucini *et al.* (2010). The effect of

seasonality on site revisitation was assessed using daily rainfall data from various sites in KNP. Because rainfall was very erratic, we calculated the mean rainfall within a 60-day moving window. The average amount of rainfall in the 60-day period after the visit was used as covariate in the analyses, representing the suitability for plant regrowth after the initial visit. Although the choice for the two-months running mean is arbitrary, the results are likely to be very similar for analyses conducted using for example a 30-day or 90-day moving window, because of their high correlation with the 60-day moving average (correlation 60-day vs. 30-day moving average: Pearson's $r = 0.929$, $n = 2132$, $P < 0.001$; correlation 60-day vs. 90-day moving average: Pearson's $r = 0.950$, $n = 2102$, $P < 0.001$).

For the ease of visualization and interpretation, as well as to facilitate the analyses, we classified these covariates into binary variables, using the lower and upper tertiles. Hence, we used the variables distance to water (dW), classified into close to water dW = 0 for sites closer than 500 m from the nearest water source) and far from water (dW = 1, > 1.75 km), tree cover (TC), classified into low tree cover (TC = 0, ≤ 28% ground cover) and high tree cover (TC = 1, > 40% ground cover), and average rainfall in the 60 days after the visit (R), classified into a dry (R = 0, ≤ 0.9 mm/day) and wet period (R = 1, > 3.9 mm/day).

To assess the influence of sex, rainfall, distance to water and tree cover on the re-visitation rate by elephants in our study area, we included all covariates, including their interaction terms, into a Cox PH model. We included a gamma-distributed frailty term to account for an unobservable random effect shared by the locations visited by the same elephant (Oakes 2001). We used Schoenfeld and Cox-Snell residuals to test for the appropriateness of the PH assumption and to test the overall adequacy (Grambsch & Therneau 1994; Bradburn *et al.* 2003b). All analyses were carried out using the software R (R Development Core Team 2009) and the Survival library (Therneau 2009).

Results

Comparison to null models

Compared to the observed movement paths, the randomized movement paths with the same mathematical properties had a rate of revisitation 0.22 times that of the observed elephants (Fig. 4.1), a difference that was statistically significant (t-test, $n = 43$, $t = -24.9$, $P < 0.001$).

The Cox PH models showed that the rate of site revisitation in areas with a high density of visited sites was 1.61 times higher than that in areas with only few visited locations, a difference that was significant (Fig. 4.1; $P = 0.001$, $z = 3.81$, $n = 40424$). The revisitation rate in areas with many revisits relative to number of visits, was 4.01 times higher than that in areas with relatively only few revisits ($P < 0.001$, $z = 41.5$, $n = 40424$). The interaction between these two factors was not significant ($P = 0.790$, $z = 0.27$, $n = 40424$).

The influence of covariates on site revisitation

Combining all covariates, including sex, into one Cox PH model was not justified, because the assumption of proportionality of hazards did not hold for sex. Hence, we analysed the patterns of site revisitation for male and female elephants separately. The Schoenfeld residuals showed no trend over time, suggesting that the PH assumption was valid for analyses done separately by sex. The cumulative hazard showed a linear correlation
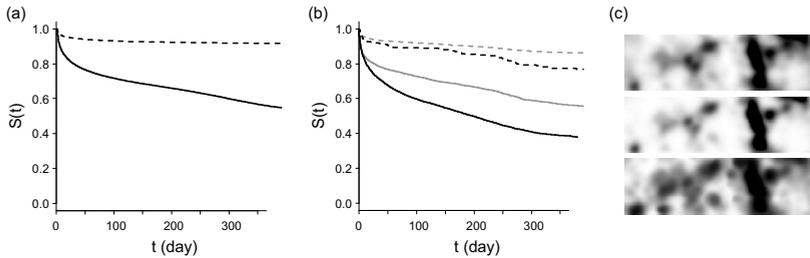
Figure 4.1: (a) Survival curves for the observed data (solid line) and randomized data (dashed line). (b) The survival curves for the observed data in relation to local density of visited sites (dashed lines for low density and solid lines for high density) and density of revisited sites relative to the number of visited sites (grey lines for low relative density and black lines for high relative density). (c) Maps of the density of visited sites (top), density of revisited sites (middle) and the proportion of visited sites that is revisited (bottom), for a random part of the study area. Black shading means high values, whereas white shading means low values.

with the Cox-Snell residuals ($r^2 = 0.99$ for the females and $r^2 = 0.95$ for the males), indicating that the overall model fit was adequate. To compare the frequency of site revisitation by male and female elephants, we analyzed the overall percentage of sites revisited between the sexes, and found no significant difference (ANOVA, $F_{1,41} = 2.444$, $P = 0.126$).

The survival curves for the patterns of site revisitation per sex in relation to the covariates are shown in Figure 4.2, and the statistics from the Cox PH regression are summarized in Table 4.1. To improve the ease of interpretation, the multiplicative effects of the covariates ($\exp\left[\sum \beta_i x_i\right]$; see Eq. 4.1) on the baseline hazard ($h_0(t)$) are shown in Table 4.2.

Both male and female elephants consistently had a higher revisitation rate for sites close to water, and visited before a dry period (Fig. 4.2; Table 4.1 and 4.2). Moreover, the male elephants always had a lower revisitation rate for sites located in high tree cover area (Table 4.2). This was not the case for the female elephants, since they had higher

Table 4.1: Summary statistics of the Cox proporional hazards models for the female and male elephants, with the covariates tree cover (TC), rainfall (R) and distance to the nearest source of surface water (dW). The covariates followed a binary classification scheme, with a value of 0 indicating low tree cover and rainfall, and close to water, whereas a value of 1 means high tree cover and rainfall, and far from water.

	Females				Males			
x	β	$\exp(\beta)$	χ^2	P	β	$\exp(\beta)$	χ^2	P
dW	-0.572	0.564	66.62	< 0.001	-0.327	0.721	5.19	0.023
R	-0.245	0.783	15.13	< 0.001	0.016	1.016	0.01	0.910
TC	0.244	1.276	16.48	< 0.001	-0.095	0.910	0.48	0.490
TC x dW	-0.285	0.752	7.98	0.005	-0.341	0.711	2.85	0.091
TC x R	0.071	1.074	0.77	0.380	-0.567	0.567	7.94	0.005
dW x R	-0.040	0.961	0.18	0.670	-0.426	0.653	4.50	0.034
TC x dW x R	-0.366	0.694	5.75	0.017	0.751	2.119	6.92	0.009
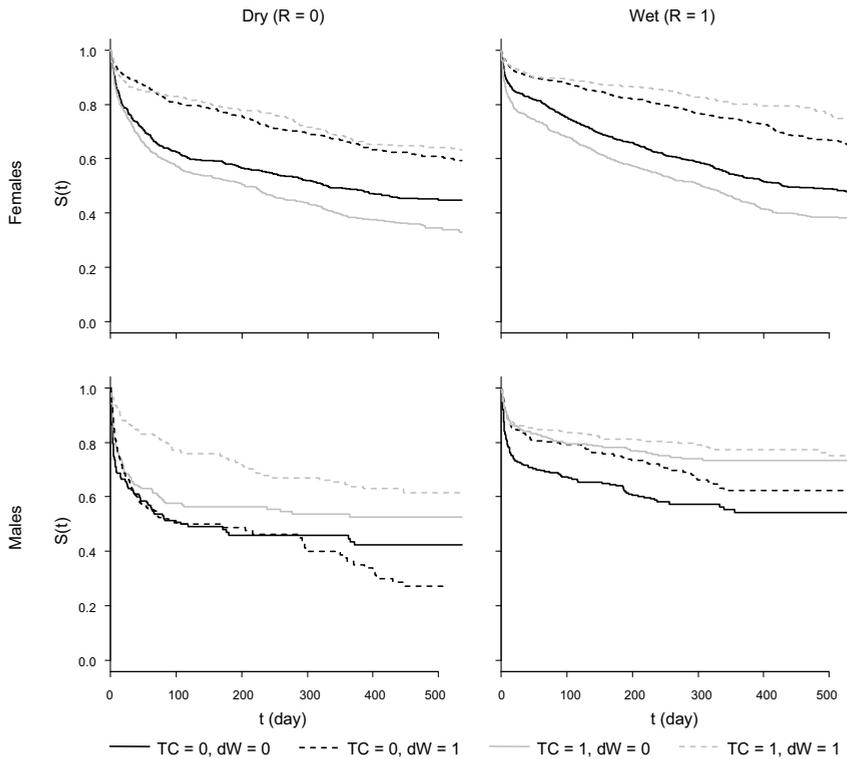
Figure 4.2: Kaplan-Meier survival curves for the male and female elephants in relation to the predictor variables tree cover (TC), rainfall (R) and distance to the nearest source of surface water (dW). The covariates were classified into binary classes, with a value of 0 indicating a low tree cover and rainfall, and close to water, whereas a value of 1 means high tree cover and rainfall, and far from water.

rates of site revisitation in high tree cover areas located close to water, both in dry and wet periods; almost equal revisitation rates for sites visited before a dry period and far from water; and lower revisitation rates in areas with high tree cover far from water during wet periods (Fig. 4.2 and Table 4.2).

Table 4.2: The influence of the covariates on the hazard rate, expressed as a multiplicative effect of $\exp\left(\sum \beta_i x_i\right)$ on the baseline hazard, $h_0(t)$, see Eq. 4.1.

		Females		Males	
		dW = 0	dW = 1	dW = 0	dW = 1
R = 0	TC = 0	1.00	0.56	1.00	0.72
	TC = 1	1.28	0.54	0.91	0.47
R = 1	TC = 0	0.78	0.42	1.02	0.48
	TC = 1	1.07	0.30	0.52	0.37

Discussion

In this paper, we focused on the patterns of site revisitation by African elephants in Kruger National Park, South Africa. Various reasons exist why animals revisit previously visited sites, ranging from natal experience, breeding philopatry or spatial neophobia to an increase in foraging efficiency due to renewal of plant material following defoliation (Watts 1998; De Knegt *et al.* 2008; Skarpe & Hester 2008; Wolf *et al.* 2009). Although signs of spatial neofobia and natal philopatry have been observed in African elephants (Pinter-Wollman 2009), we primarily focused on the site revisitation in relation to the two main resources for elephants, namely vegetation and water, as well as the influence of rainfall and sex on the way elephants interact with these resources. Our analyses showed that the elephants, in general, revisited sites more frequently (ca. 5 times) than could be expected based on chance alone (Fig. 4.1a), supporting our first hypothesis. Hence, the elephants selectively visit and revisit specific sites in the study area. Overall, ca. 35% of the visited sites were revisited. These findings are in line with those of Loarie *et al.* (2009a) and Wolf *et al.* (2009), who showed that elephants and elk (*Cervus canadensis*), respectively, exhibited signs of site fidelity.

Our analyses indicate that habitat preference potentially independent of past experience, as well as fidelity to specific areas, influenced the revisitation rate of the elephants (Fig. 4.1b). Namely, sites are more often revisited when they are in a preferred area, yet within preferred areas, certain sites are revisited only few times (Fig. 4.1b). Likewise, some sites within areas that are visited only few times are revisited often, in relative terms, whereas other sites within these areas are revisited only few times (Fig. 4.1b). This shows that areas preferred by the elephants are frequently revisited, perhaps for the same reason they were visited in the first place, but also that this generalization does not hold everywhere, since several sites are revisited more often (or less often) than can be expected from the number of visits. Additional processes are thus at work to create spatial heterogeneity in the patterns of site fidelity by the elephants.

An important environmental characteristic that influences the patterns of site fidelity by the elephants is surface water availability. The results supported our hypotheses that elephants have higher rates of revisitation to sites close to water and visited in dry periods. Sources of surface water are a key determinant of elephant movements (e.g., Harris *et al.* 2008; Van Aarde *et al.* 2008). Because they are distributed spatially as discrete localities, and because elephants need to drink regularly, elephants visit almost daily one of these water sources so that such sites are being revisited frequently. During the dry season, when numerous water sources have dried up, the remaining sources of water attract even more elephants and consequently are revisited even more frequently. Thus, the elephants roaming in areas centered around water sources, and even more so during the dry season when elephants range less widely around water sources (Van Aarde *et al.* 2008), might be the mechanism behind our finding that the revisitation rate increases close to water and in the dry season.

Proximity to surface water thus proved to be an important factor in determining the patterns of site fidelity by the elephants, especially in periods when surface water was limited. Furthermore, tree cover also influenced the patterns of site revisitation, albeit differently so between male and female elephants. The male elephants consistently had a lower rate of site revisitation in areas with a high tree cover, regardless of whether these areas are close to water or not, or whether the sites were visited during dry or wet periods. The female elephants, on the other hand, consistently revisited sites with

high tree cover more frequently when these sites were located close to a source of surface water. Yet, far from water, the female elephants were indifferent regarding the rate of site revisitation in relation to tree cover during dry periods, but revisited site less frequently in high tree cover during wet periods.

The positive association between tree cover in areas close to water and the rate of site revisitation by female elephants agrees with observations by Ntumi *et al.* (2005) and Thomas *et al.* (2008) that elephants prefer closed canopy habitat types like riparian vegetation and vegetation types associated with water. This could be due to the higher moisture availability in riverine areas that permit the riparian vegetation to grow faster or longer, or remain green longer in the season, offering a better quality browse (Smit *et al.* 2007a). During the wet season, moisture for plant growth is more widely available, so that the elephants roam over more extensive areas and are less restricted by surface water. Areas close to water might thus be important for elephants because of the proximity to surface water, but also because of the vegetation associated to water. Hence, these areas supply the elephants with resources (forage and water), but also shelter under the more dense vegetation (Smit *et al.* 2007a).

The fidelity to specific sites by the female elephants was thus dependent upon the vegetation, proximity to water and rainfall, including their interactions. However, the male elephants showed strong patterns in relation to surface water, rainfall and tree cover alone. This might indicate that the female elephants, who forage in breeding groups led by a matriarch (McComb *et al.* 2001), adjust their pattern of site revisitation taking into account a combination of environmental and climatic conditions, perhaps more than the male elephants did. Thus, although we did not find an overall difference in the percentage of sites revisited, their patterns of site revisitation differed in relation to environmental and climatic conditions. Females are smaller, have a higher reproductive input and live in permanent groups with many young individuals, resulting in a feeding approach that maximizes nutritional intake through selective foraging (Stokke 1999; Stokke & Du Toit 2000; Shannon *et al.* 2006a). As timely revisiting specific areas might increase the nutritional quality of the vegetation and increase the amount of forage within reach of the young individuals by keeping the vegetation in a hedged state, the female elephants might have a stronger incentive to revisit specific areas because of herbivore-vegetation feedbacks than male elephants, who can tolerate lower food quality and can access a larger portion of the woody vegetation because of their larger size, but also by physically manipulating the vegetation through tree-pushing or breaking off branches (Smallie & O'Connor 2000; Shannon *et al.* 2006a).

A need for further research includes a more detailed and mechanistic linkage between the patterns of site revisitation and the structure of the vegetation. Several studies have shown that elephants are major agents in manipulating the vertical structure of the vegetation, and possibly the aerial cover of the woody vegetation (e.g., Ben Shahar & Macdonald 2002; Smallie & O'Connor 2000; Calenge *et al.* 2002; Augustine & McNaughton 2004). In our study, we used estimates of aerial tree cover derived from remotely sensed imagery. It may thus be possible that the driving mechanisms behind site revisitation (i.e., an adjustment of the vertical structure of the vegetation through foraging), was thus not picked up by our analyses. Further research thus needs to be done that includes this vertical dimension of the vegetation, for example through the use of new approaches that integrate high-resolution imaging spectroscopy and light detection and ranging (LiDAR) to provide large-scale, quantitative insight into the vertical dimension of the vegetation

(e.g., Asner *et al.* 2009). Moreover, field observations may yield additional insights in mechanisms behind revisitation patterns.

This paper highlights the importance of considering factors other than purely exogenous environmental variables in explaining space use by free ranging herbivores, since past use of specific sites may influence the present-day observed spatial patterns. Past use of certain areas may lead to spatial memory and thus the efficiency with which animals can exploit their resources, it may also initiate positive herbivore-vegetation feedbacks that promote the revisitation of previously visited sites. We conclude that familiarity with specific sites influences the movements and habitat selection by African elephants, patterns of which are mediated by seasonally varying abundance of surface water and growth of vegetation.

*HJ de Knegt, F van Langevelde, MB Coughenour, AK Skidmore,
WF de Boer, IMA Heitkönig, NM Knox, R Slotow, C van der
Waal & HHT Prins*

5

Spatial autocorrelation and the scaling of species-environment relationships

*I*ssues of residual spatial autocorrelation (RSA) and spatial scale are critical to the study of species-environment relationships, because RSA invalidates many statistical procedures, while the scale of analysis affects the quantification of these relationships. Although these issues independently are widely covered in literature, only sparse attention is given to their integration. This paper focuses on the interplay between RSA and the spatial scaling of species-environment relationships. Using a hypothetical species in an artificial landscape, we show that a mismatch between the scale of analysis and the scale of a species' response to its environment leads to a decrease in the portion of variation explained by environmental predictors. Moreover, it results in RSA and biased regression coefficients. This bias stems from error-predictor dependencies due to the scale mismatch, the magnitude of which depends on the interaction between the scale of landscape heterogeneity and the scale of a species' response to this heterogeneity. We show that explicitly considering scale effects on RSA can reveal the characteristic scale of a species' response to its environment. This is important, because the estimation of species-environment relationships using spatial regression methods proves to be erroneous in case of a scale mismatch, leading to spurious conclusions when scaling issues are not explicitly considered. The findings presented here highlight the importance of examining the appropriateness of the spatial scales used in analyses, since scale mismatches affect the rigor of statistical analyses and thereby the ability to understand the processes underlying spatial patterning in ecological phenomena.

Introduction

Understanding the relationships between organisms and their environment is of paramount importance for understanding the mechanisms behind (spatial) variation in ecological phenomena (Currie 2007; De Knegt *et al.* 2007, 2008; McIntire & Fajardo 2009). Critical to this understanding are issues of pattern and scale (Levin 1992), because two general characteristics inherent to ecological data can complicate analyses of species-environment relationships. First, ecological phenomena are often spatially autocorrelated, leading to problematic statistical inference if left unaccounted for (Cliff & Ord 1981; Legendre 1993; Dormann *et al.* 2007). Second, organismal response to environmental cues hinges on the scales that individuals can perceive and respond to, leading to sensitivity in the quantification of species-environment relationships to the spatial perspectives chosen (Levin 1992; Wu 2007; Mayor *et al.* 2009). Hence, the importance of spatial autocorrelation (SAC) and spatial scale in the study of species-environment relationships has stimulated much research over the past decade. Unfortunately, integration between these fields has been limited, although different processes may create SAC at different scales depending on the scales of an organism's response to its environment (Wagner 2004; Wagner & Fortin 2005). Here, we attempt to facilitate the integration between these important issues, as we argue that their interaction offers possibilities to achieve a more thorough understanding of species-environment relationships.

Ecological data may exhibit SAC due to "endogenous" (or "inherent") community or demographic processes (e.g., dispersal, conspecific attraction), or spatial dependence of organisms to the underlying environmental conditions that are spatially structured (i.e., 'exogenous' or "induced" SAC; Cliff & Ord 1981; Legendre 1993). If the sources of SAC are not fully accounted for in analyses (due to failure to include an important environmental driver, inadequate capture of its nonlinear effect, or failure to account for endogenous processes), the unexplained spatial pattern will appear in the residual errors, leading to residual spatial autocorrelation (RSA). Consequently, the assumption of independently and identically distributed (i.i.d.) errors common to most statistical procedures is violated, creating biased Type I error estimates due to inflation of degrees of freedom (Clifford *et al.* 1989; Legendre *et al.* 2002). Moreover, parameter estimates may be biased or their sign even inverted (Lennon 2000; Kuhn 2007; Bini *et al.* 2009).

Recent studies analyzing the scale-sensitivity of species-environment relationships have formed the idea that species have "characteristic scales" of response to their environment (Dormann & Seppelt 2007). These studies typically analyze the importance of landscape characteristics by regressing response data against landscape variables measured at various spatial scales (i.e., ambit radii) around sampling locations (e.g., Van Langevelde 2000; Steffan-Dewenter *et al.* 2002; Holland *et al.* 2004; Mayor *et al.* 2007). Hence, the influence of the scale of landscape context (i.e., the characteristics of the landscape surrounding a site) on the phenomenon under study is being investigated (Brennan 2002). However, these studies generally do analyze neither the spatial structure of the environmental predictors (Dormann & Seppelt 2007) nor the spatial structure in the model residuals (i.e., RSA).

Yet, since organisms respond to environmental characteristics at specific (but often unknown) scales, the spatial patterns resulting from a species' response to extraneous predictors may differ from the spatial structure of the landscape (Wagner & Fortin 2005). This potentially leads to RSA and problematic inference when the scale of analysis does not match the scale at which the focal species responds to its environment (Gotway &

Young 2002). Thus, in order to account for the sources of SAC in ecological phenomena, scaling issues need to be considered. Moreover, because understanding the mechanisms that maintain the observed spatial patterns critically depends on our ability to decompose the spatial pattern into the contributions of different processes affecting it (Legendre *et al.* 2009), understanding the interactions between SAC and the spatial scaling of species-environment relationships is urgently required. Although several authors have studied the influence of the scale of environmental SAC on analyses of organismal response (e.g., Lennon 2000; Beale *et al.* 2007; Hawkins *et al.* 2007; Diniz-Filho *et al.* 2007), analyses regarding the influence of the scaling of a species' response to exogenous predictors on RSA have not yet been carried out.

This paper therefore focuses on the interplay between RSA and the spatial scaling of species-environment relationships. We use a hypothetical species and artificial environmental data to examine this interplay by making statistical issues explicit. The use of artificial data allows us to vary, independently, the scale of analysis, the scale of the species' response, and the scale of environmental heterogeneity, as well as to control the relationship between the species and its environment. We frame our analyses around three central issues: (1) the link between RSA and the spatial scale of analysis, given the scale of a species' response and the scale of environmental heterogeneity, (2) the consequences of a scale mismatch for parameter estimation in regression analyses, and (3) the robustness of several spatial regression methods, devised to account for the effects of RSA, when analyzing data at incorrect scales.

Methods

A virtual dataset

We used the dataset of Dormann *et al.* (2007), which contains a regular grid with 1108 cells and two artificial explanatory variables: "rain" and "jungle cover", hereafter referred to as R and D, respectively. The predictor variables are based on an elevation model of the Maunga Whau Volcano in New Zealand, where R is highly dependent on elevation (including a rain-shadow in the east) and thus strongly autocorrelated, whereas D is dominated by a high noise component (Fig. 5.1; Dormann *et al.* 2007). The two variables are uncorrelated (Pearson's $r = 0.013$, $n = 1108$, $P = 0.668$), thus avoiding model instability due to correlated predictors. Both predictors were normalized to zero mean and unit variance prior to analyses.

We distributed a hypothetical species over this landscape based on the two predictor variables, while setting the spatial scale of its response. We did this by averaging the predictor variables in a circular focal neighbourhood (or moving window) centered on each grid cell, with ambit radius or buffer size f. Hence, we refer to "scale" here as the radius within which the predictor variables are measured, thus being a measure of the area or inference space represented by each data point.

To simplify the modelling process and interpretation, we distributed the virtual species based on R with $f = 0$, thus using only local grid cell information; however, its response to D was modelled using a radius of 3 cells (D_f, with $f = 3$; Fig. 5.1). Spatial scaling of the species' response to D is not associated to a specific spatial causation here, but one could interpret the species' response to D in relation to, for instance, proximity to nesting sites, risk contagion due to proximity of habitats associated to predators, or the ability to detect predators.
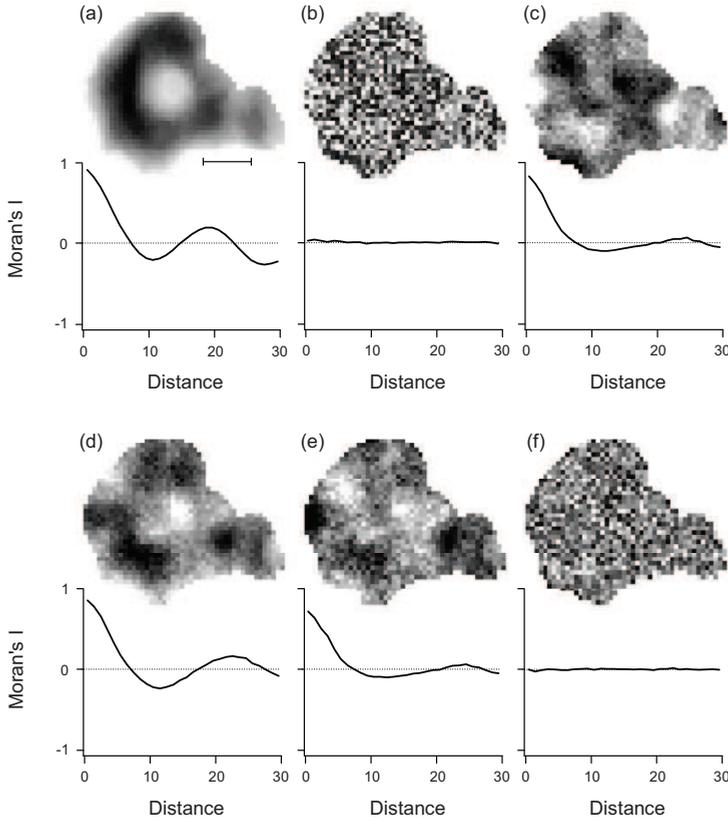
Figure 5.1: Maps and corresponding correlograms for the predictor and response variables: (a) rain (R); (b) jungle cover (D); (c) D averaged within a circular focal neighbourhood with a radius of 3 distance units (i.e., D_f with $f = 3$); (d) simulated density of our hypothetical species (y; Eq. 5.1 and 5.2); (e) residuals of an OLS model using only local information (i.e., R and D); (f) residuals of an OLS model using local and contextual information at the correct scales (i.e., R and D_f with $f = 3$). The scale bar in (a) depicts 10 distance units.

The abundance (y) of the virtual species in each grid cell was modelled as:

$$y = \beta_0 + \beta_1 R + \beta_2 D_f + \varepsilon \quad \text{with} \quad \varepsilon \sim \text{N}(0, \sigma^2) \tag{5.1}$$

where $\beta_0 = 15$, $\beta_1 = 1$, $\beta_1 = -4.29$, $f = 3$, and ε is a spatially uncorrelated (i.i.d.) Gaussian error term ("white" noise). We choose the parameter values in such manner that both predictors exerted equal influence on the response variable (i.e., equal standardized coefficients). We conducted analyses where we changed the signal-to-noise ratio, through varying the variance of the error term relative to the variance of the deterministic part of Eq. 5.1, such that $\sigma_{error} : \sigma_{determinisitc} = 0.10$, 0.25 or 0.50.

Analyses

We analyzed the abundance of our virtual species by regressing it against the two environmental predictor variables using ordinary least-squares (OLS) regression, and compared

the parameter estimates to their "true" values for different scenarios. We used all grid cells in the statistical analyses. The spatial patterns in the residuals were examined using residual maps and correlograms that plot Moran's *I* coefficients (e.g., Fortin & Dale 2005) as a function of separation distance between paired observations up to a distance of 30 distance units (Fig. 5.1). All analyses were carried out in the statistical software R (R Development Core Team 2009), using the libraries spdep (Bivand 2009), ncf (Bjornstad 2009), nlme (Pinheiro *et al.* 2008) and RandomFields (Schlather 2008).

Spatial scaling and RSA

In order to make the link between SAC and the spatial scaling of species-environment relationships explicit, we write Eq. 5.1 equivalently as a spatial cross-regressive model. Essentially, Eq. 5.1 is a non-spatial regression model augmented by a cross-regressor in the form of a spatially lagged explanatory variable:

$$y = \beta_0 + \beta_1 R + \beta_3 D + \lambda WD + \varepsilon \tag{5.2}$$

where λ is the regression coefficient of the spatially lagged predictor D connected through the spatial weight matrix W (here a row-standardized binary contiguity matrix with non-zero elements if the distance between grid cell centroids is less than or equal to 3 distance units), $\beta_3 = \beta_2/(n+1) \approx -0.17$ and $\lambda = n\beta_2/(n+1) \approx -4.12$, where n is the number of neighbourhood cells. Hence, the species' response to its environment does not only depend on the characteristics within the grid cell (R and D, hereafter referred to as "local" environmental characteristic), but also on the characteristics of the surrounding landscape regarding D up to a distance of 3 distance units (i.e., WD; the "landscape context" or neighbourhood). We can thus refer to β_3 and λ as the respectively local and contextual landscape effects regarding D.

Hence, correlating the distribution of our virtual species to the predictor variables using only local information leads to the omission of the effect of landscape context (WD). Thus, the actual regression becomes:

$$y = \beta_0 + \beta_1 R + \beta_3 D + \mu \quad \text{where} \quad \mu = \varepsilon + \lambda WD \tag{5.3}$$

Consequently, the statistical model is misspecified, because it is inconsistent with the data-generating process (Eq. 5.1 and 5.2). The error term μ contains the omitted variable (WD), thus any spatial pattern in WD will be reflected in the residual errors, leading to RSA. Alternatively, analyzing the distribution of our virtual species in relation to both predictors while including the effect of landscape context regarding D, but at a scale larger than the species' scale of response to D, leads to spatial smoothing of data and hence RSA (Gotway & Young 2002; Keitt *et al.* 2002; Diniz-Filho *et al.* 2003; Dormann 2007).

Thus, a mismatch between the spatial scale of analysis and the scale of organismal response results in misspecification of the statistical model and RSA. Hence, we expect that plotting the level of RSA as function of the scale of analyses provides a clue regarding the characteristic scale of the species' response to its environment: that is the scale where the level of RSA is minimized. We therefore analyzed the distribution of our virtual species in relation to both R and D, using only local information regarding R, while varying the buffer size for predictor D from 0 up to 6 distance units. At each scale, the predictors D_f (with $f = [0\text{-}6]$) are uncorrelated with R (all Pearson's $| r | < 0.035$ and

$P > 0.2$, $n = 1108$). Following Kissling and Carl (2008), we quantified the total level of RSA (RSA_{tot}) as the summation of the absolute Moran's *I* values of the correlogram up to a distance of 30 distance units. Furthermore, we also analyzed Akaike's information criterion (AIC) values for the different scales. Note that the analyses carried out at different scales were not independent tests, but served to determine at which scale RSA_{tot} and AIC were minimized. We replicated these analyses 1000 times, each time with a different realization of the error term ε.

Scale effects on parameter estimation

In spatially structured landscapes, the presence of spatially lagged explanatory predictors can induce correlation between predictors (in our case between *D* and W*D*), even if the environmental predictors themselves (*R* and *D*) are uncorrelated (Haining 2003). This could encumber analyses and threaten their statistical and inferential interpretation (Graham 2003). Thus, besides resulting in RSA, model misspecification due to the erroneous omission of spatially lagged predictors is a typical example of the omitted variable problem in a spatial context (Florax & Folmer 1992). Consequently, the OLS estimator of the regression coefficients may be biased, the residual variance overestimated, and inference procedures invalid (Florax & Folmer 1992; Anselin *et al.* 2004).

In the case of our virtual species, the local information regarding *D* and its spatially lagged counterpart W*D* are only moderately correlated (Pearson's $r = 0.09$, $n = 1108$, $P = 0.002$). However, as even low levels of correlation between predictors can bias analyses (Graham 2003), we expect that analyzing our virtual species in relation to *R* and *D* while omitting W*D* results in an over-estimation of the regression coefficient for *D*.

Moreover, the level of correlation between local and spatially lagged predictors depends on the scale at which a species responds to the environmental predictors and is modified by the scale of SAC of the landscape variable (i.e., Gotway & Young 2002; Wong 2009). Hence, the bias that results from omitting a spatially lagged predictor depends on both the scale of environmental SAC and the scale of the species' response to the environmental predictor. To quantify this bias, we simulated landscapes similar in function as *D*, but with a varying spatial scale of SAC, which we refer to as the "dominant scale" (DS) of landscape heterogeneity (e.g., De Knegt *et al.* 2008). Then, through omitting the spatially lagged predictor and comparing the estimated regression parameters to their "true" values, we quantified the influence of the interaction between the DS of landscape heterogeneity and the scale of organismal response on the regression analyses. We simulated landscapes with a DS of 0.5, 2 and 10 distance units, and a virtual species whose scale of response (*f*) to the simulated landscapes ranged from 1 to 6 distance units (with an i.i.d. error term with $\sigma_{error} : \sigma_{determinisitc} = 0.1$). For each combination of DS and *f*, we quantified: (1) the correlation between local and contextual information; (2) the difference in AIC values (ΔAIC) between a spatial model with landscape context at the correct scale and a non-spatial model that uses only local information; (3) the difference in regression coefficients between the non-spatial and spatial OLS models ($\Delta\beta = \beta_{OLSns} - \beta_{OLSs}$); and (4) the total level of RSA when omitting landscape context as measured by RSA_{tot}. All analyses were iterated 1000 times, with different realizations of the simulated landscapes and error term.

Dealing with RSA resulting from a scale mismatch

Ecologists facing RSA commonly rely on regression-based approaches that are intended either to live with the problem (e.g., by spacing sampling locations further apart, adjust-

ing the degrees of freedom, or adjusting the effective sample size; see e.g., Dutilleul *et al.* (1993), Holland *et al.* (2004), Fortin & Dale (2005)), or to model the spatial process causing the autocorrelation as part of the regression analysis. The latter approach allows a correction of the parameter estimates, and resulted in the development of various forms of spatial regression that are increasingly becoming part of the standard toolbox for ecologists. Given their wide-spread use, we tested several of these techniques for their reliability in estimating the species-environment relationships when analyzing the distribution of our hypothetical species. We confined ourselves to two techniques widely used in ecological studies: methods based upon simultaneous autoregression (SAR) and generalized least squares (GLS); and a relatively new and emerging spatial approach belonging to the class of eigenvector-based spatial filtering techniques: spatial eigenvector mapping (SEVM). We refrain from technical discussion of these techniques here and only provide a nontechnical synopsis, since many of them have received exhaustive review, comparison and discussion elsewhere (Cliff & Ord 1981; Keitt *et al.* 2002; Fortin & Dale 2005; Schabenberger & Gotway 2005; Griffith & Peres-Neto 2006; Dormann 2007; Dormann *et al.* 2007; Kissling & Carl 2008; Anselin 2009; Bini *et al.* 2009).

SAR models operate with spatial weight matrices (viz. W in Eq. 5.3) that specify the strength of interaction between neighbouring sites. Depending on where this spatial interaction is thought to occur, SAR models specify the relationship between the response variable (SAR-lag) or residual errors (SAR-error) at each location and those at neighbouring locations (Anselin 2002; Schabenberger & Gotway 2005; Dormann *et al.* 2007; Anselin 2009). As demonstrated by Kissling & Carl (2008), the performance of SAR models depends on the neighbourhood distance and coding styles of the spatial weight matrices used. Because it is difficult to decide a priori which neighbourhood structure is most efficient, Kissling & Carl (2008) recommended to test a wide variety of SAR model specifications, and to identify the best model based on AIC and RSA_{tot}. Hence, we fitted both SAR-lag and SAR-error models using 5 different neighbourhood sizes (1 to 3 distance units with increments of 0.5) and 3 coding styles (binary, row-standardized and variance-stabilized), and used both AIC and RSA_{tot} to evaluate these model specifications.

Methods based on GLS include spatial interaction in the regression model by incorporating SAC explicitly into the variance-covariance structure, assuming a parametric correlation function as estimated from a semi-variogram of the OLS residuals (Keitt *et al.* 2002; Dormann *et al.* 2007). Three frequently used correlation functions are exponential, Gaussian and spherical representations (Dormann *et al.* 2007). We analyzed our dataset using these three representations, and evaluated their performance using AIC and RSA_{tot}.

Eigenvector-based spatial filtering techniques seek to avoid the complications involved in estimating autoregressive parameters, as well as to exploit established OLS theory. They are based on the eigenfunction decomposition of spatial connectivity matrices, either binary or distance-based (Griffith & Peres-Neto 2006; Dormann *et al.* 2007). The resulting spatial filters translate the spatial arrangement of data points into explanatory variables that capture spatial effects at different scales, which can be included in regression analyses to capture the dependencies among the residuals (Borcard & Legendre 2002; Borcard *et al.* 2004; Diniz-Filho & Bini 2005; Griffith & Peres-Neto 2006; Tiefelsdorf & Griffith 2007). We used the distance-based eigenvector procedure as described by Griffith & Peres-Neto (2006) and Dormann *et al.* (2007), and included eigenvectors as

spatial predictors into the linear model until RSA was no longer significant at $\alpha = 0.05$.

We used the above-mentioned spatial regression methods to analyze the distribution of our virtual species when only using local information (Eq. 5.3). We iterated the analyses of the SAR and GLS models 1000 times, each time with a different realization of the error term (with $\sigma_{error}:\sigma_{determinisitc} = 0.10$). However, the analyses using SEVM were iterated 100 times, since these were computationally intensive. We compared the parameter estimates to their "true" values, assessed model fit using AIC, and checked for residual SAC using RSA_{tot}. Moreover, we tested how the different spatial methods behave in case of a scale mismatch under varying DS and f, with DS = 0.5, 2 and 10 distance units and f ranging from 2 to 6 distance units, in a similar fashion as described above, while analyzing the deviance of the estimated regression coefficients from their true values ($\Delta\beta$). We iterated each combination of DS and f 500 times for the SAR and GLS models, yet 15 times for SEVM, due to its time-consuming computations.

Results

Spatial scaling and RSA

When omitting WD, only 51% of the variation was explained by the predictor variables (Appendix A), and the residuals exhibited strong SAC (Table 5.1, Fig. 5.1e). Because WD is uncorrelated with R (Pearson's $r = 0.034$, $n = 1108$, $P = 0.261$) the OLS estimator was unbiased regarding the influence of R ($\beta_1 \approx 1$; Table 5.1). However, since WD is correlated to D, the erroneous omission of WD led to an overestimation of the influence of D: $\beta_3 \approx -0.25$ (cf. -0.17; Eq. 5.2, Table 5.1). Including both R and D in the analysis, while varying the scale of analysis for D, showed a pronounced scale-dependency of RSA_{tot} (Fig. 5.2). The scale where RSA_{tot} was minimized corresponds to the scale at which the virtual species was set to respond to D, i.e., a buffer size of 3 cells. Only when analyzing the distribution of our virtual species at this scale could 99% of the variation be explained by the predictor variables (Appendix A), while yielding the i.i.d. noise that we included in Eq. 5.1 and 5.2 (Fig. 5.1f), as well as the correct estimates of regression coefficients (Table 5.1). A scale mismatch thus not only induced RSA, but also reduced overall model fit as measured by AIC (Fig. 5.2).

A larger contribution of the noise term led to lower levels of RSA_{tot} in case of a scale mismatch (Fig. 5.2), since it was set to be i.i.d. However, RSA_{tot} and AIC showed similar patterns in their dependency on the scale of analysis in qualitative terms. The level of RSA as measured by RSA_{tot} showed no dependency on the signal-to-noise ratio when our virtual species was analyzed at the correct scale.

Scale effects on parameter estimation

The correlation between the local and contextual information increased with increasing DS of landscape heterogeneity, yet decreased with increasing scale of a species' response (Fig 5.3). This was due to the increase in environmental SAC with increasing DS, while the similarity between observations separated in space decreased with increasing f. Consequently, the difference in model fit between a spatial and non-spatial model (ΔAIC) showed exactly the opposite pattern, because erroneously omitting landscape context resulted in less information loss with increasing DS or decreasing f.

The bias in regression coefficient ($\Delta\beta$) when erroneously omitting the influence of landscape context resulted from a trade-off between the level of correlation between local and contextual information on the one hand, and the relative influence of the omitted

Table 5.1: Summary statistics of the regression models analyzed using 1000 iterations (except for SEVM: 100 iterations). The unstandardized regression coefficients (mean±SEM) refer to Eq. 5.2, and I is the Moran's I coefficient for the first distance class. The top-row shows the regression parameters for the correct model (i.e., landscape context included at the correct scale), whereas the other rows depict models that use only local information. The significance levels are based on the number of iterations yielding significant effects (with $\alpha = 0.05$, ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.1$, ns: non-significant).

| Model	β_0	β_1	β_3	λ	AIC	RSA_{tot}	I
Spatial OLS	15.00±0.00013***	1.00±0.00014***	-0.165±0.00013***	-4.11±0.0173***	-1105.6±1.49	0.19±0.00089	-0.003±0.00049[ns]
Non spatial OLS	14.99±0.00013***	0.97±0.00014***	-0.253±0.00013***		3100.3±0.29	3.90±0.00106	0.710±0.00009***
GLS	15.05±0.00026***	1.00±0.00048***	-0.007±0.00015[ns]		1500.0±0.75	0.44±0.00067	-0.079±0.00015[ns]
SAR-error	15.00±0.00020***	0.93±0.00055***	-0.014±0.00015[ns]		1547.6±0.72	0.34±0.00046	-0.071±0.00013[ns]
SAR-lag	1.18±0.00120***	0.15±0.00009***	-0.033±0.00014*		1584.4±0.70	0.30±0.00047	-0.057±0.00013[ns]
SEVM	14.99±0.00043***	0.80±0.00090***	0.019±0.00041*		1391.3±2.22	0.32±0.00201	0.006±0.00028[ns]
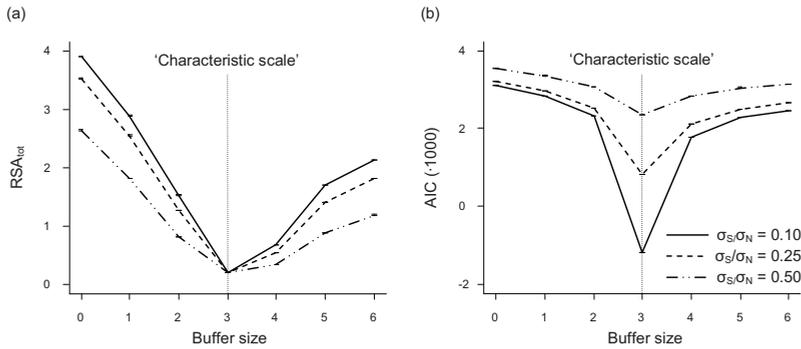
Figure 5.2: Model diagnostics as function of the spatial scale used while regressing the species' distribution against D: (a) RSA_{tot}, i.e., the summation of absolute Moran's I values up to a distance of 30 units; and (b) Akaike's information criterion (AIC) values. The different lines represent different signal-to-noise ratios (σ_S/σ_N). Means ($\pm$ SEM) are shown based on 1000 iterations. The vertical dotted lines represent the scale at which the virtual species was set to respond to its environment.

variable in determining the response variable on the other hand. With increasing f, the importance of landscape context relative to the focal cell increased, whereas the level of correlation decreased. Hence, since the level of correlation between local and contextual characteristics was positively linked to DS, $\Delta\beta$ showed a hump-shaped response relative to f, and increased with increasing DS (Fig 5.3).

Dealing with RSA resulting from a scale mismatch

For the SAR models, a neighbourhood structure with row-standardized coding for a distance of 1.5 cells (a "queen" contiguity matrix) explained the data best, yielding the lowest AIC and RSAtot values for all tested specifications. For the GLS models, a spherical relationship between the error term and geographical distance gave the best performance as measured by AIC and RSA_{tot}. Below, we report only the results using the best configuration for each modelling approach. The results are summarized in Table 5.1.

All spatial models were able to reduce RSA to non-significant levels and simultaneously yielded lower AIC values than the OLS model when omitting WD. However, they also showed bias (i.e., underestimation) in the estimated magnitude of the effect of D on the abundance of our virtual species, with SEVM even estimating a positive relationship as opposed to the true negative relationship. Although most tested methods yielded appropriate estimates of the intercept and the effect of R on the species' abundance, application of SAR-lag yielded shifts in both estimates.

Analyses of the distribution of our virtual species, with varying f and DS, in relation to only local information using the spatial methods showed that the bias in regression coefficients ($\Delta\beta$) varied between the different methods used, and depended on both f and DS for GLS and SEVM. The SAR models performed relatively well in landscapes with large DS, yet, in relative terms, their estimates were still more than 30% off. Note that comparing the different spatial methods to the results of a non-spatial OLS drastically changes the results, yet both the non-spatial OLS as well as the tested spatial regression methods essentially used a mis-specified model to estimate the species-environment relationships.
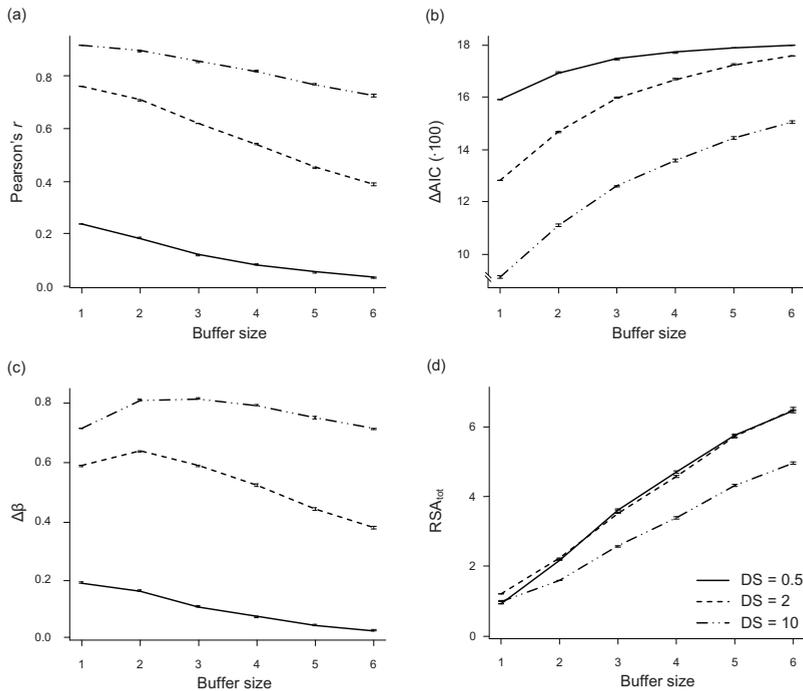
Figure 5.3: Interactions between the spatial scale of a species' response (buffer size) and the spatial scale of SAC in the environmental predictor (DS): (a) the correlation (Pearson's *r*) between local and contextual information; (b) the difference in Akaike's information criterion (AIC) values between a spatial (i.e., with landscape context at the correct scale) and non-spatial (i.e., using only local information) model; (c) the difference in regression coefficients between a spatial and non-spatial model; and (d) the total level of RSA (RSA_{tot}) when omitting landscape context. Means ($\pm$ SEM) are shown based on 1000 iterations.

Discussion

In this paper, we have focused on the influence of a scale mismatch on the estimation of species-environment relationships, as it is important to understand the way such analyses are affected by the use of data at inappropriate scales (Gotway & Young 2002). Our analyses show that a scale mismatch leads to a reduction in the part of variation explained by landscape predictors and induces RSA. Although RSA is often seen as problematic, it implies structure in the residuals and therefore information about the processes not captured by the current model (Haining 2003; Fortin & Dale 2005; McIntire & Fajardo 2009). Thus, RSA is something one might not want to discard or correct for: the problem is not its presence, but the absence of an explanation (Cliff & Ord 1981; Dormann 2007). Unfortunately, while RSA can be quantified, its origins cannot directly be identified: it may be the end product of an amalgam of interacting processes, with different processes creating patterns that may be observationally equivalent (Wagner & Fortin 2005; Anselin 2009).
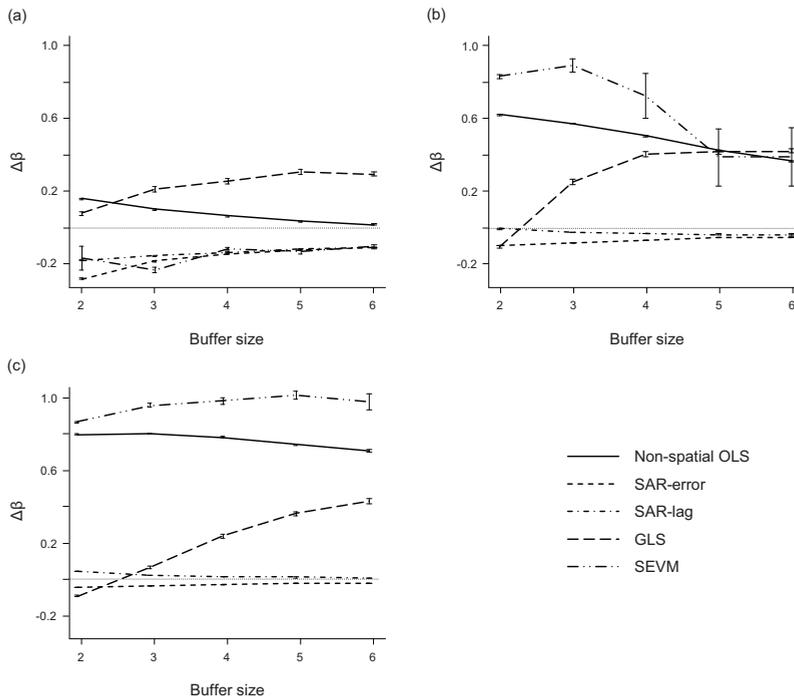
Figure 5.4: Deviance of the coefficient estimates from their "true" values, for different models using only local information (abbreviations as used in the text), as function of the scale of a species' response, and for landscapes with a scale of autocorrelation (DS) of (a) 0.5; (b) 2; and (c) 10 distance units. Means (± SEM) are shown based on 500 iterations (except SEVM: 15 iterations).

Inferring relevant scales from residuals

As shown above, analyzing response data erroneously using only local information is essentially a type of model misspecification due to an omitted variable problem. This omitted variable, W*D* in case of our virtual species, contains two scale components: (i) the spatial structure of the landscape predictor *D* that is included at the wrong scale and (ii) the spatial scale of the species' response to the predictor as captured by W. Hence, the pattern of RSA is the result of the interaction between these scale components, thus the scale of species-environment relationships cannot directly be inferred from spatial patterns in the residuals alone (Wagner & Fortin 2005; Dormann 2009), even when RSA exclusively stems from a scale mismatch.

However, because RSA can bear the fingerprint of a scale mismatch, varying the scale of analysis while analyzing RSA can reveal the scale of the species' response (Fig 5.2). Using scales larger or smaller than the scale of a species' response leads to spatial smoothing or the omission of landscape context, respectively. While the influence of spatial smoothing on RSA has been noted by other authors (Gotway & Young 2002; Keitt *et al.* 2002; Diniz-Filho *et al.* 2003; Dormann *et al.* 2007; Tiefelsdorf & Griffith 2007), the influence of omitting landscape context has received only sparse attention (but see Florax & Folmer 1992; Wagner & Fortin 2005). In the following, we will therefore focus on this issue.

Parameter shifts

Besides leading to RSA, erroneously ignoring landscape context leads to a biased OLS estimator. However, this is not the result of RSA, but due to the non-zero covariance between regressor (*D*) and error (*μ*; Eq. 5.3) stemming from the correlation between local (*D*) and contextual (W*D*) information (Table 5.1, Fig. 5.3). This leads to the violation of one of the assumptions of regression analyses (i.e., zero covariance between the explanatory variables and error term), and therefore to overestimation of the parameter of interest and henceforth faulty conclusions (Ebbes *et al.* 2005; Luskin 2008). Note that OLS residuals (but not the errors) are, by definition, uncorrelated to the predictors; this violation is thus difficult to diagnose. Moreover, the magnitude of the regressor-error correlation is dependent on the scale of landscape heterogeneity, as well as on the scale of the species' response (Fig. 5.3).

While several authors have argued that RSA may well bias coefficient estimation (e.g., Lennon 2000; Dormann 2007; Kuhn 2007), other studies found non-spatial OLS models to be robust and unbiased (Diniz-Filho *et al.* 2003; Beale *et al.* 2007; Hawkins *et al.* 2007). Our findings support the latter view, since we found unbiased coefficient estimates under RSA for predictors uncorrelated to the error term. This is consistent with statistical literature (Cressie 1991; Legendre *et al.* 2002; Schabenberger & Gotway 2005; Hawkins *et al.* 2007; Tiefelsdorf & Griffith 2007). Note, however, that there is no doubt that RSA inflates the chance of type I errors, so that coefficients obtained by OLS are not minimum variance estimators (Fortin & Dale 2005; Hawkins *et al.* 2007).

Dealing with RSA resulting from a scale mismatch

Since RSA due to a scale mismatch is an issue of data analysis, constrained by the resolution and extent of the data, analyzing the data at appropriate scales suffices as remedial action against RSA and the error-regressor dependency. This is where our simulations diverged from those of other studies on the influence of SAC on regression analyses (e.g., Dormann 2007; Kissling & Carl 2008). These studies typically focus on endogenous SAC by adding an aggregation mechanism to the error term such that it is uncorrelated with the predictor variables (Dormann 2009), and conclude that making a correction for RSA through applying one of the spatial regression methods is important since these show good type I error control and precise parameter estimation (e.g., Keitt *et al.* 2002; Dormann *et al.* 2007; Kissling & Carl 2008).

However, although all our tested spatial methods yielded a better model fit than non-spatial OLS and decreased RSA to insignificant levels, parameter estimation turned out to be problematic in case of a scale mismatch. All tested methods underestimated the influence of *D*, both in terms of regression coefficient as well as significance. Why our analyses yielded biased coefficient estimates has a dual explanation. First, GLS and SEVM, like OLS, suffer from space-environment confounding when the error term is correlated with a regressor (Ebbes *et al.* 2005; Griffith & Peres-Neto 2006; Ayinde 2007; Hawkins *et al.* 2007; Kissling & Carl 2008; Luskin 2008; Betts *et al.* 2009). Second, the spatial methods test for marginal effects of environmental predictors after controlling for SAC due to an unknown spatial process, thereby leading to a reduction in the strength of environmental effects if the response is controlled by exogenous predictors (Segurado *et al.* 2006; Currie 2007).

Our simulations thus emphasize what several authors (Lennon 2000; Haining 2003; Wagner 2004; Anselin 2006; Van Teeffelen & Ovaskainen 2007; Dormann 2009) warned

against: using "rough and ready" methods to improve model fit can yield "rough and ready" answers that may be quite wrong. Moreover, even the most advanced and computer-intensive statistical procedures are no guarantee for improving our understanding of ecological responses, as such methods often do not give straightforward information about the underlying processes (Borcard *et al.* 2004; Dormann *et al.* 2007). Thus, spatial regression methods should not be used as a quick fix for modelling spatial data: as the species-environment relationships are scale-dependent and this is not incorporated in the analysis, this may be a more severe threat to the interpretation of RSA than an inflated Type I error (Haining 2003; Wagner 2004; Van Teeffelen & Ovaskainen 2007). Discounting the results of non-spatial OLS in favor of that of spatial models when the coefficients differ is thus not tenable (Bini *et al.* 2009).

Differentiating the sources of SAC

Instead, researchers should focus on the sources of RSA and hence on what causes the differences between spatial and non-spatial methods. Although little emphasis has been put on disentangling the sources of RSA (Van Teeffelen & Ovaskainen 2007), understanding species-environment relationships can only be achieved by distinguishing between endogenous and exogenous SAC (Wagner & Fortin 2005; Fortin & Melles 2009). This is mostly done by partitioning the spatial pattern into a pure environmental component, a pure spatial component, a partition shared by environmental and spatial influence, and an unexplained portion (Borcard *et al.* 1992, 2004; Legendre *et al.* 2005, 2009; Peres-Neto *et al.* 2006; Laliberté *et al.* 2009). Scale influences the amount of variation explained by environmental predictors (Legendre *et al.* 2009; Laliberté *et al.* 2009), where erroneously ignoring landscape context leads to a downward-biased contribution of environmental predictors and an upward-biased contribution of pure spatial influences (Appendix A). Consequently, conclusions regarding the contributions of exogenous and endogenous processes based on such analyses are thus scale-dependent: a scale mismatch leaves room for the inference that endogenous processes are at play even when only exogenous factors are driving the response variable. Much weight thus rests upon rationales used in the selection of appropriate spatial scales; yet they are often selected based on data availability, convenience, or our human perception of the system (Mayer & Cameron 2003; Dormann 2007; Wheatley & Johnson 2009).

Generality and caveats

Although we have framed our analysis in terms of the relationships between species distributions and landscape predictors, our arguments are not limited to such analyses only, but apply to a large array of ecological investigations where ecological responses are regressed against landscape predictors. Our analyses were kept simple for the purpose of demonstration, yet more complex analyses can be conducted within the framework outlined above, e.g., by including distance-decay relationships in the specification of the spatial weight matrix W. However, we do not claim that explicitly considering scale effects necessarily increases our understanding of ecological phenomena, since ecological analyses are mostly correlative and are thus not strict inferential tests of causality: they can only suggest potential explanatory factors (Diniz-Filho *et al.* 2003). Moreover, cross-scale correlations can confound the interpretation of species-environment relationships, since predictors at one scale might be correlated with predictors at other scales (Mayor *et al.* 2007).

Conclusion

We conclude that a scale mismatch decreases the portion of spatial variation explained by landscape predictors, while elevating the level of RSA and thereby obstructing inferential tests. Moreover, it leads to error-regressor correlations resulting in problematic parameter estimation. Because accurately describing the strength and significance of species-environment relationships is central to understanding the functioning of ecosystems, conserving biodiversity and managing ecosystems, we argue that explicitly considering scaling issues should be part of the formal framework within which proper estimation and inference are carried out. Doing so could contribute to a better understanding of spatial patterns in ecological phenomena by avoiding false inferences. The simplicity, power and many important potential applications make the approach outlined above a useful addition to ecologists' toolbox.

Appendix A

Using a commonly used approach to assess the contribution of environmental and spatial predictors on spatial ecological responses (see e.g., Borcard *et al.* 1992, 2004), we partitioned the distribution of our hypothetical species (*y*, see Eq. 5.1 and 5.1) into spatial and environmental contributions. We analysed the case where we omitted the influence of landscape context (i.e., W*D*, here referred to as the non-spatial model), and compared that to the case where we included landscape context regarding *D* at the correct scale (here referred to as the spatial model).

Following other authors (e.g., Borcard *et al.* 2004; Legendre *et al.* 2009), we represented the spatial structure of the artificial landscape using eigenvectors of the spatial connectivity matrix as described by Griffith & Peres-Neto (2006) and Dormann *et al.* (2007). Following Borcard *et al.* (2004) and Legendre *et al.* (2009), only eigenvectors with positive eigenvalues were used.

We partitioned the distribution of our virtual species into environmental and spatial contributions (e.g., Borcard *et al.* 1992, 2004, see Fig. 5.5): [a] pure environmental: the fraction of *y* explained by the environmental predictors independently of any spatial structure; [b] shared environmental and spatial: the spatial structuring in *y* that is shared by the environmental data, i.e., the contribution of spatially structured environmental variation; [c] pure spatial: the spatial patterns in *y* that are not shared by environmental data but can be explained by the spatial relationships as captured by the spatial eigenvectors; [d] unexplained: the fraction of *y* explained neither by environmental data nor by spatial relationships.

The spatial predictors (i.e., the eigenvectors) explained 96% of the variation in *y*, while the environmental predictors explained 99% of the variation in the case of the
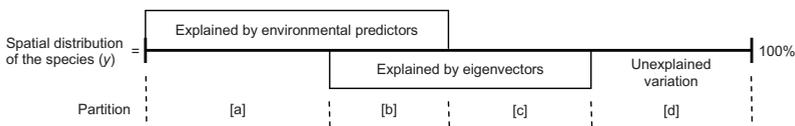
Figure 5.5: Partitioning of the variation of species distribution data (*y*) between environmental and spatial predictor variables. The figure is adapted from Borcard *et al.* (1992) and Legendre *et al.* (2009).
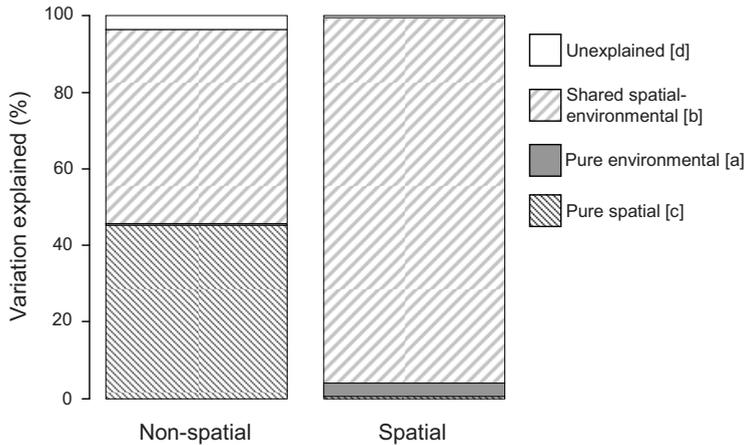
Figure 5.6: Partitioning of the variation in the distribution of our virtual species in case of the non-spatial and spatial models. The letters between square brackets correspond to the partitioning as explained in the text and depicted in Fig. 5.5.

spatial model, but just 51% in the case of the non-spatial model. The contributions of the four fractions per model are shown in Fig. 5.6.

Note that the contributions of the partitions show a major difference between the spatial and non-spatial model. Most importantly, the contribution of the environmental predictors (pure environmental or shared environmental-spatial) decreases when using the non-spatial model (i.e., a scale mismatch), while the contribution of the pure spatial part shows a major increase. This can have major consequences for conclusions regarding the contribution of exogenous and endogenous processes based on such analyses.

De Knegt, HJ, F van Langevelde, AK Skidmore, A Delsink, R Slotow, S Henley, G Bucini, WF de Boer, MB Coughenour, CC Grant, IMA Heitkönig, M Henley, NM Knox, EM Kohi, E Mwakiwa, BR Page, M Peel, Y Pretorius, SE van Wieren & HHT Prins

6

The spatial scaling of habitat selection by African elephants

Understanding and accurately predicting the spatial patterns of habitat use by organisms is becoming increasingly important for ecological research, biodiversity conservation and ecosystem management, yet the effects of spatial scale pose a formidable challenge for such understanding. We therefore assessed the influence of environmental context, varied over an appreciable range of scales, on the analysis and prediction of habitat selection by African elephants in Kruger National Park, South Africa. The inclusion of environmental context at appropriate spatial scales improved the quantification of habitat selection, and increased the predictive capacity of habitat suitability models. The elephants responded to their environment in a scale-dependent, and perhaps hierarchical manner, with forage characteristics driving habitat selection at coarse spatial scales, and surface water at fine spatial scales. The elephants exhibited sexual segregation regarding habitat selection, mainly in relation to their response to vegetation and topography, where male elephants preferred areas with high tree cover but avoided areas with much herbaceous biomass, whereas this pattern was reversed for the female elephants. This paper shows that the spatial distribution of animals can be better understood, and hence predicted, when scale-dependent species-environment relationships are explicitly taken into account.

Introduction

Ecology is fundamentally concerned with understanding the relationships between organisms and their environment. Because spatial scale influences these relationships, the influence of scale on the mechanisms explaining habitat selection is currently highly debated (Senft *et al.* 1987; Levin 1992; Wiens 2002; Wheatley & Johnson 2009). Scale is usually expressed in terms of *resolution* and *extent*, and no question in spatial ecology can be answered without referring explicitly to these components at which data are measured or analysed (Turner *et al.* 1989; Wiens 1989, 2002). Beyond resolution and extent, the importance of spatial context is increasingly being recognised (Guisan & Thuiller 2005; Guisan *et al.* 2006; Wheatley & Johnson 2009), because habitat selection may not only depend on site-specific characteristics, but also on the characteristics of the landscape surrounding a site: the so-called *environmental context* (Holland *et al.* 2004; Guisan & Thuiller 2005; Guisan *et al.* 2006). This raises a third scale-component, namely the *range* (i.e., ambit radius) at which environmental context influences habitat selection by animals.

Since we often have no *a priori* knowledge about the scales at which species respond to environmental heterogeneity, it is important to identify characteristic scales of this response in order to avoid a mismatch between the scale(s) used for analyses, and the one(s) at which habitat selection occurs (Schooley 2006; Mayor *et al.* 2007; Wheatley & Johnson 2009; De Knegt *et al.* 2010). If different components of scale (resolution, extent or range) are changed simultaneously, one cannot decouple the importance of each if patterns change among observational scales (Wheatley & Johnson 2009). However, analyzing how species-environment relationships depend on the range of environmental context, within the constraints set by the resolution and extent of the data, may provide the solution required to study the spatial scaling of species-environment relationships, as it may provide clues as to which scales are ecologically most relevant to the species of interest (Van Langevelde 2000; Holland *et al.* 2004; Johnson *et al.* 2004; Guisan & Thuiller 2005; Schooley 2006; Mayor *et al.* 2007). Yet, the scales of analyses are often chosen arbitrarily with no biological connection to the system of study (Mayer & Cameron 2003; Wheatley & Johnson 2009), and the number of ambit radii used, if any, is often limited (e.g., Boscolo & Metzger 2009; Brady *et al.* 2009; Ibánez *et al.* 2009; Janssen *et al.* 2009, but see Pinto & Keitt 2008; Schmidt *et al.* 2008; Drapela *et al.* 2008).

When better understanding the scale at which environmental context influences habitat selection, the predictive capacity of species distribution models can be increased. In recent years, such models have become an important tool to address issues in research, biodiversity conservation and management (Guisan & Thuiller 2005; Guisan *et al.* 2007), and they are especially important for decisions regarding threatened species (e.g., black rhinoceros - *Diceros bicornis*) or those that play an important biotic role in the ecosystem (e.g., African elephants - *Loxodonta africana*; Shannon *et al.* 2008). In this paper, we study the influence of the spatial scaling of environmental context on habitat selection by African elephants in Kruger National Park, South Africa. We focus specifically on the scaling of the elephants' response to food and water resources, since these are known to be key determinants of elephant distribution (Chamaille-Jammes *et al.* 2007a,b; Smit *et al.* 2007a,c,b; Harris *et al.* 2008; Shannon *et al.* 2008; Van Aarde *et al.* 2008). We aim at testing whether the explicit consideration of environmental context at appropriate scales improves the description and predictability of habitat selection by elephants. We differentiate between dry and wet season habitat selection, since water is widely available during

the wet season, whereas seasonal water sources dry up in the dry season (Van Aarde *et al.* 2008). Moreover, since several authors have observed sexual differences in foraging ecology of elephants (Stokke 1999; Stokke & Du Toit 2000, 2002; Greyling 2004; Shannon *et al.* 2006b, 2010; Smit *et al.* 2007c), we analyse habitat selection by male and female elephants separately. By doing so, we aim at increasing our understanding of the mechanisms behind elephant distribution, and demonstrate methods to study the spatial scaling of habitat selection.

Methods

Study area and species

Kruger National Park (KNP) is South Africa's largest nature reserve, covering roughly 19000 km^2 and harbouring close to 14000 elephants. Besides linking habitat selection by the elephants in KNP to the distribution of food and water resources, we also included topographic and climatic variables in our analyses, as these have also been shown to influence space usage by elephants (Nellemann *et al.* 2002; Wall *et al.* 2006; Van Aarde *et al.* 2008). All environmental variables were inserted into a geographic information system (GIS) and formatted to a regular grid with 1 km resolution for the entire KNP (Fig. 6.1).
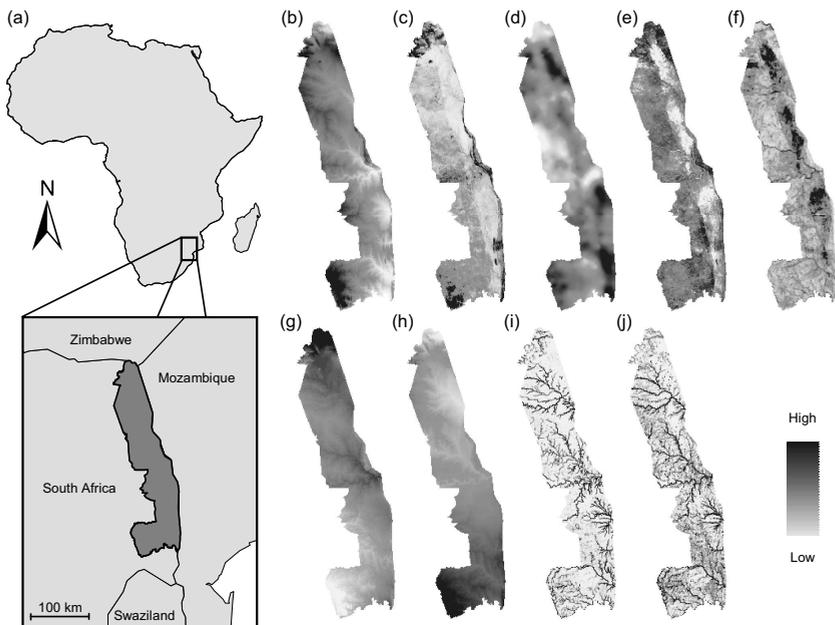

Figure 6.1: (a) The location of the study area, and maps of some environmental variables: (b) elevation, (c) slope, (d) herbaceous biomass, (e) tree cover, (f) vegetation heterogeneity, (g) mean annual temperature, (h) mean annual rainfall, (i) water occurrence and (j) water permanency. The variables are mapped at a resolution of 1 km^2.

Vegetation characteristics

The two structural components of the vegetation in our study area, namely the tree and herbaceous vegetation, were used in our analyses. The tree cover (TC; woody plants taller than 1.3 m) was estimated from combined optical (Landsat ETM+) and radar (JERS-1) imagery calibrated with field data, as described by Bucini *et al.* (2010). It resulted in a 90-m resolution woody cover map, yet for our analyses, we averaged the TC across each 1 km^2 grid cell. The herbaceous biomass (HB) data layer resulted from interpolating field records from various sites across the park (with $n = 533$; Smit *et al.* 2007c). Since vegetation heterogeneity has also been identified as a determinant of elephant distribution (Grainger *et al.* 2005; Murwira & Skidmore 2005), we included the coefficient of variation of TC across each 1 km^2 grid cell in our analyses, thereby being a proxy for the structural vegetation heterogeneity (VH).

Surface water availability

Six perennial rivers cross the park from west to east, while 14 ephemeral rivers only contain surface water during a large part of the wet season (Smit *et al.* 2007c). In addition, KNP contains around 300 water points (pans and artificial boreholes). Using data on rivers and water points, dry and wet season distance-to-water layers were created, calculated as the Euclidean distance of the centroid of each grid cell to the nearest water source. The artificial water points and perennial rivers were assumed to carry water year-round, whereas the ephemeral rivers and pans were assumed to have water only during the wet season. Since other studies found elephants in the study area to be more attracted to the river system than to artificial water points (Smit *et al.* 2007c; Grant *et al.* 2008), we differentiated between distance to the nearest water carrying river (dR), distance to the nearest water point (dWP) or distance to the nearest source of water regardless of which type (dW). Furthermore, we used aerial census data of surface-water sightings in each 1 km^2 grid cell over a 17 year period (1981-2001, excl. years 1985 and 1994-1996). These data resulted in a water occurrence (WO) data layer: the number of surface water sightings per km^2 over the 17-year period, and a water permanency (WP) data layer; the number of years in which a specific grid cell contained at least one water occurrence record.

Topography and weather conditions

A 90 m resolution Shuttle Radar Topography Mission (SRTM) elevation model (Jarvis *et al.* 2008) was used to represent the surface elevation across KNP, ranging from 100 m to 840 m a.s.l. The mean elevation (Elev) and slope (Slope) in each 1-km^2 grid cell were used in the analyses. We used the WorldClim dataset (Hijmans *et al.* 2007) to represent the weather conditions in the study area. Mean annual rainfall (Prec) varied from 400 mm to 940 mm and mean annual temperature (Temp) varied from 19.5°C to 24.5°C.

Elephant occurrence data

Data on elephant habitat use was obtained from 43 elephants (18 males and 25 females) deployed with global positioning system (GPS) collars (Hawk105 collars, Africa Wildlife Tracking cc., South Africa). As even long sampling intervals do not guarantee independence between data points, the best strategy is to use the shortest possible sampling interval over the longest possible period (Rooney *et al.* 1998; Cushman *et al.* 2005). Hence, we recorded locations at hourly intervals over a 4 year period (2005-2008), resulting in

245,427 recorded locations. The precision of the GPS fixes was assessed using points ($n = 11244$) recorded when the collars were located at known locations: the Skukuza and Tanda Tula research stations. The deviations from the centre of gravity of these locations followed a bivariate normal distribution (*x*-directional normality: $P = 0.300$, *y*-directional normality: $P = 0.279$, *x-y* correlation: Pearson's $r = 0.08$), with 95% of the points situated within 27.8 m from the sites' geometric centroids.

General approach

We analysed habitat selection by comparing the environmental variables of used sites (i.e., those at the recorded GPS locations) to the reference conditions in the study area. This parallels the Grinnellian concept of *ecological niche*, defined here as the sub-space of species occurrences within the hyperspace defined by the environmental variables (both abiotic and biotic) of the area considered to be available to the species of interest (the *ecological space*; Hirzel *et al.* 2002; Soberón 2007; Hirzel & Le Lay 2008; Soberón & Nakamura 2010). Following Loarie *et al.* (2009b), we considered the area within a distance of 1 day of travel (ca. 10 km) around the recorded locations to be available to the elephants. This was done separately for female and male elephants, avoiding spurious analyses with artificially inflated test statistics when data are drawn from too large an area (VanDerWal *et al.* 2009). The high mobility of the elephants, the conservative extent that we used, and the long time frame over which GPS locations were recorded, suggests that the entire area we considered available to the elephants was indeed likely to be "available" to them. Moreover, the long-term (spatial) memory of elephants (e.g., McComb *et al.* 2001; Hakeem *et al.* 2005; Van Aarde *et al.* 2008) suggests that the area we considered to be available was also "known" to the elephants. In the following, we refer to this area as the available area or study area, thereby omitting parts of KNP that were to far from the recorded GPS positions (e.g., the far north and south of KNP).

We used the Mahalanobis distance statistic (D^2; Mahalanobis 1936; Rotenberry *et al.* 2006), the frequently-used ecological-niche factor analysis (ENFA; Hirzel *et al.* 2002) and the Mahalanobis distance factor analysis (MADIFA; Calenge *et al.* 2008; Calenge & Basille 2008) to study the patterns of habitat selection by elephants in the study area. We first used Mahalanobis D^2 to quantify the response of the elephants to food and water resources as function of the range of environmental context considered. We then included all environmental variables into the ENFA and tested whether the explicit consideration of environmental context at appropriate scales increased the quantified level of habitat selectivity. Lastly, we predicted habitat suitability within the available area using the MADIFA, and tested whether the inclusion of environmental context at appropriate scales increased the predictability of habitat selection in the study area. Throughout, we analysed the patterns of habitat selection separately for male and female elephants, and differentiated between patterns in the dry season (Jun-Aug), and a wet season (Dec-Feb). All analyses were carried out using the software R (R Development Core Team 2009) and the package Adehabitat (V1.7.3; Calenge 2006), and they are further discussed below.

Spatial scaling of environmental context

The Mahalanobis distance statistic quantifies the standardized difference between locations in the ecological space and the centroid of the ecological niche, taking into account the structure of the ecological niche (Rotenberry *et al.* 2006; Calenge *et al.* 2008). The more similar in environmental conditions a location is to the centroid of the ecological

niche (the species' mean), the smaller is D^2, and the more suitable the habitat at that location (Rotenberry *et al.* 2006; Calenge *et al.* 2008; Calenge & Basille 2008; Etherington *et al.* 2009). Conversely, a larger D^2 indicates a greater dissimilarity to the species' mean. Hence, we used the mean D^2 over the available area ($\bar{D}^2$) as measure of the level of habitat selectivity regarding an environmental variable, and analysed the dependency of $\bar{D}^2$ to the range of environmental context considered.

We varied the range of environmental context by averaging the environmental predictor variables HB, TC, WO and WP within circular focal neighbourhoods, centred on each site, while varying the ambit radius (Brennan *et al.* 2002; Holland *et al.* 2004; De Knegt *et al.* 2010). We varied the ambit radius from 0 km (thus essentially no environmental context and hence only site-specific information) up to 40 km, with 1 km increments (viz. the resolution of the data). For each of the environmental variables ($n = 4$) and each of the buffer sizes ($n = 41$), we measured $\bar{D}^2$. Following other authors (Holland *et al.* 2004; Schaefer & Mayor 2007), we refer to the buffer size with the highest $\bar{D}^2$ as the *characteristic scale* of response to the environmental variable considered.

If such characteristic scales are found, the elephants might respond to their environment at these specific scales, or it might represent the spatial scales of environmental heterogeneity with which the elephants are forced to cope (Wheatley & Johnson 2009). To distinguish between the two, we quantified the environmental heterogeneity regarding HB, TC, WO and WP using variograms that plot the degree of spatial variation as function of separation distance between paired observations (Fig. 6.2a). The distance where the variogram levels off (the "range" of the variogram) is of interest here, because it gives information regarding the dominant scale of spatial variation (Murwira & Skidmore 2005; De Knegt *et al.* 2008). Through comparing the dominant scales of environmental heterogeneity to the characteristic scales of elephant response, we can draw conclusions about the elephants following spatial patterns in the landscape, or the elephants selecting environmental variables at biologically meaningful scales, in which case the dominant scales of the landscape and the characteristic scales of habitat selection differ.

Ecological niche factor analysis

We included all environmental variables in subsequent ENFA analyses, with HB, TC, WO and WP at the characteristic scales (which we will refer to as "spatial" analyses). We compared the results of ENFA analyses including these variables, with those from ENFA analyses where the influence of environmental context was not considered (i.e., the "non-spatial" analyses). ENFA quantifies the dissimilarity between ecological niche and ecological space in terms of *marginality* and *specialization*, where marginality is defined as the standardized difference between the centroids of the ecological space and the ecological niche, whereas specialization is defined as the narrowness of the ecological niche relative to the ecological space (Hirzel *et al.* 2002; Basille *et al.* 2008; Calenge & Basille 2008). Marginality itself expresses some specialization: the higher the marginality, the higher is the specialization (Hirzel *et al.* 2002; Basille *et al.* 2008). ENFA complements analyses based on Mahalanobis distances, as it allows identification of the part of the Mahalanobis distances corresponding to specialization and marginality (Calenge *et al.* 2008).

ENFA extracts information regarding the ecological niche by computing new, uncorrelated factors: one marginality axis and several axes of specialization (Hirzel *et al.* 2002). All environmental variables are scored for their contribution to each axis, with coeffi-

cients ranging from -1 to +1. Positive marginality coefficients indicate that the centroid of the ecological niche is higher (for negative values lower) than the average conditions in the study area, indicating preference for higher values (for negative values avoidance). Only the absolute value of the specialization coefficients is meaningful: a high value indicates a narrow niche breadth in comparison with the ecological space (Hirzel *et al.* 2002). The eigenvalue associated to any axis expresses the amount of specialization it accounts for, thus the variance of the ecological space divided by the variance of the ecological niche on this axis (Hirzel *et al.* 2002).

Besides coefficients per environmental variable, overall values of marginality (M) and specialization (S) were calculated, providing general clues about the degree of niche restriction, where M ranges from 0 to 1 and indicates how far the ecological niche is from the average conditions in the study area, and S ranges from unity to infinity and indicates the breadth of the niche, with high values indicating narrow niches (Hirzel *et al.* 2002, 2004; Calenge & Basille 2008). Following Basille *et al.* (2008), we used bi-plots projecting both the ecological niche and the environmental variables on the subspace defined by the first two axes of the ENFA to interpret the results. We used a Monte Carlo randomisation procedure with 1000 permutations, randomizing the elephant locations within the study area, to test the significance of M and S.

Model prediction and evaluation

To test whether the explicit consideration of environmental context at appropriate scales improved the predictability of elephant distribution in the study area, we compared the predictability of spatial and non-spatial models. While the ENFA is often used to create habitat suitability (HS) maps (e.g., Hirzel *et al.* 2002; Hirzel & Arlettaz 2003; Engler *et al.* 2004; Hirzel *et al.* 2004; Tsoar *et al.* 2007), it is not recommended to combine the ENFA axes into a single measure of HS, because they do not all have the same mathematical status (Calenge & Basille 2008). We therefore used the MADIFA to compute HS maps, since D^2 combines marginality and specialization into one single measure of habitat selection while its factorial decomposition allows the computation of reduced-rank Mahalanobis distances (Rotenberry *et al.* 2006; Calenge & Basille 2008). We used the first 5 MADIFA axes, because not all available n axes define ecologically relevant measures of HS, but reflect the *a priori* decision by the investigator to include n environmental variables (Rotenberry *et al.* 2006). This avoids overfitting while retaining most information regarding habitat selection (Calenge *et al.* 2008; Calenge & Basille 2008).

We evaluated the HS models using a k-fold cross-validation procedure (with $k = 10$). We used $k-1$ parts to calibrate the model while computing the evaluation on the left-out partition (Austin 2002; Boyce *et al.* 2002; Johnson *et al.* 2006; Hirzel *et al.* 2006). This procedure was repeated k times, each time leaving out another partition. The evaluation was done using the method described by Boyce *et al.* (2002): the ratio (O/E) of the observed (O) number of evaluation points within a HS class relative to the expected (E) number of evaluation points in case of random habitat use is plotted against the midpoint HS value. As binning and classification issues become problematic, Hirzel *et al.* (2006) developed a continuous version of this method, with the O/E ratio computed within a moving-window (with size w) along the HS gradient. We used $w = 0.2$ for a gradient of HS values ranging from 0 (highly unsuitable) to 1 (highly suitable).

This procedure produces k curves of O/E versus HS, providing three levels of information regarding the predictability of HS. First, the variance among the curves gives

information about model robustness along the HS range. Second, if the O/E ratio increases with increasing HS, the model has a good predictive ability (Hirzel *et al.* 2006). We used the Spearman rank correlation coefficient (ρ) of the mean O/E ratio with HS to quantify the consistency of the HS model, with high values of ρ in case of a monotonically increasing O/E curve, indicating a good model (Boyce *et al.* 2002; Hirzel *et al.* 2006). Although an ideal model would have a linear O/E curve, meaning that HS is proportional to the probability of use (Manly *et al.* 1993), real curves may exhibit non-linear (e.g., exponential) or stepwise shapes (Hirzel *et al.* 2006). Third, the maximum value of the O/E curve reflects how much the model differs from chance expectation (i.e., O/E = 1), thereby reflecting the model's ability to differentiate the characteristics of the species' niche from those of the studied area (Hirzel *et al.* 2006).

Results

Spatial scaling of environmental context

The strength of habitat selection as quantified by $\bar{D}^2$ was highly dependent on the range of environmental context considered (Fig. 6.2). For all gradients, $\bar{D}^2$ was lower at a buffer size of 0 km (i.e., without environmental context) than when including environmental context, at most scales considered. All gradients (except for TC and WO for female elephants in the dry season and TC, WO and WP for females in the wet season) showed a distinct single maximum $\bar{D}^2$ for a buffer size > 0 km and < 40 km, i.e., the characteristic scales. The gradients for TC regarding female elephants showed a clear minimum $\bar{D}^2$ at a buffer size of ca. 10 km, whereas the gradients regarding WO for the female elephants showed two (local) maxima of $\bar{D}^2$: at ca. 10 km and ca. 30 km buffer size (Fig. 6.2). Male and female elephants differed strongly in their maximum $\bar{D}^2$ values and characteristic scales for the HB and TC gradients (Fig. 6.2). The dominant scales of spatial variation regarding the examined environmental variables (Fig. 6.2a) did not match the characteristic scales of the elephants' response to these environmental variables (Fig. 6.2b), suggesting that the scale at which the elephants responded to the environment predictors examined here did not follow the scales at which environmental heterogeneity was most dominant.

Habitat selection analyses

The Monte-Carlo randomization tests showed that the ENFA axes, for both spatial and non-spatial analyses, were highly significant (all $P < 0.001$). Thus, the habitat occupied by the elephants differed unequivocally from the conditions in the study area, or, in

Table 6.1: Comparing the overall ecological niche factor analysis (ENFA) statistics for a non-spatial (i.e., environmental context is not considered) and spatial (i.e., environmental context is explicitly considered; see Table 6.2) models in terms of overall marginality (M) and specialization (S). Higher values of both M and S indicate a higher level of habitat selectivity as measured by ENFA.

	Non-spatial		Spatial	
	M	S	M	S
Females dry	0.65	1.63	0.73	2.04
Females wet	0.60	1.66	0.67	2.10
Males dry	0.37	2.94	0.55	3.21
Males wet	0.37	2.65	0.61	2.83
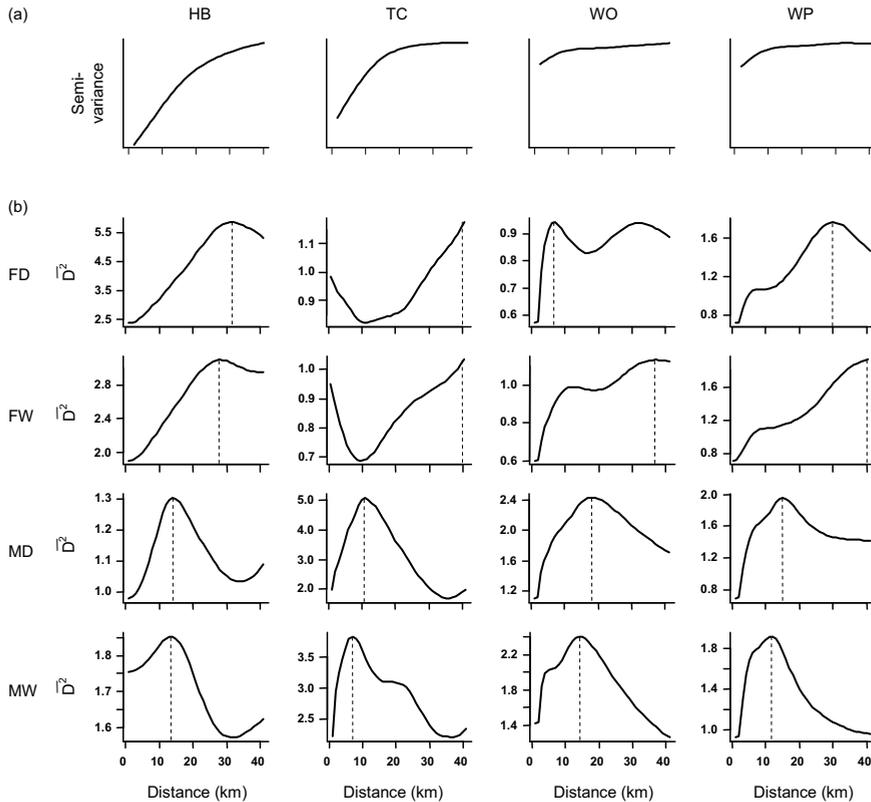
Figure 6.2: (a) Variograms expressing the spatial structure of the environmental variables herbaceous biomass (HB), tree cover (TC), water occurrence (WO) and water permanency (WP). The scales for the y-axes are omitted due to differences in measurement scales, however, they all start at zero. (b) The mean Mahalanobis distance ($\bar{D^2}$) over the available area for the environmental variables, measured at different buffer sizes for the focal area. FD: female elephants in the dry season, FW: female elephants in the wet season, MD: male elephants in the dry season, and MW: male elephants in the wet season. The vertical dotted lines indicate the characteristic scales, i.e., the buffer size where $\bar{D^2}$ is maximized.

other words, the elephants exhibited pronounced habitat selection. The spatial models that explicitly considered environmental context had higher values of M and S than the non-spatial models (Table 6.1). Including environmental context at appropriate spatial scales resulted in an increase of M of ca. 10% and S of ca. 25% for the female elephants, and an increase in M of ca. 55% and S of ca. 8% for the male elephants (Table 6.1).

The first 4 axes of the spatial ENFA analyses explained ca. 80% of all the information regarding the niche structure, that is 100% of the marginality and ca. 60% of the specialization. The marginality axes explained little of the specialization (< 7%), meaning that the niche breadth of the elephants was not particularly narrow for the variables for which their optimum was the furthest from the average conditions. The eigenvalues attributed to the first specialization axes (females: 6.8 and 9.2 for the dry and wet season, respectively; males: 12.7 and 12.6, respectively) indicated that the variance in

the environmental variables in KNP was much higher than the variance in environmental conditions experienced by the elephants, in other words: the elephants had a relatively narrow ecological niche.

The magnitude of the marginality and specialization coefficients increased in most analyses when explicitly considering environmental context at appropriate spatial scales (Table 6.2): the length of the vectors in Fig. 6.3 mostly increased when considering
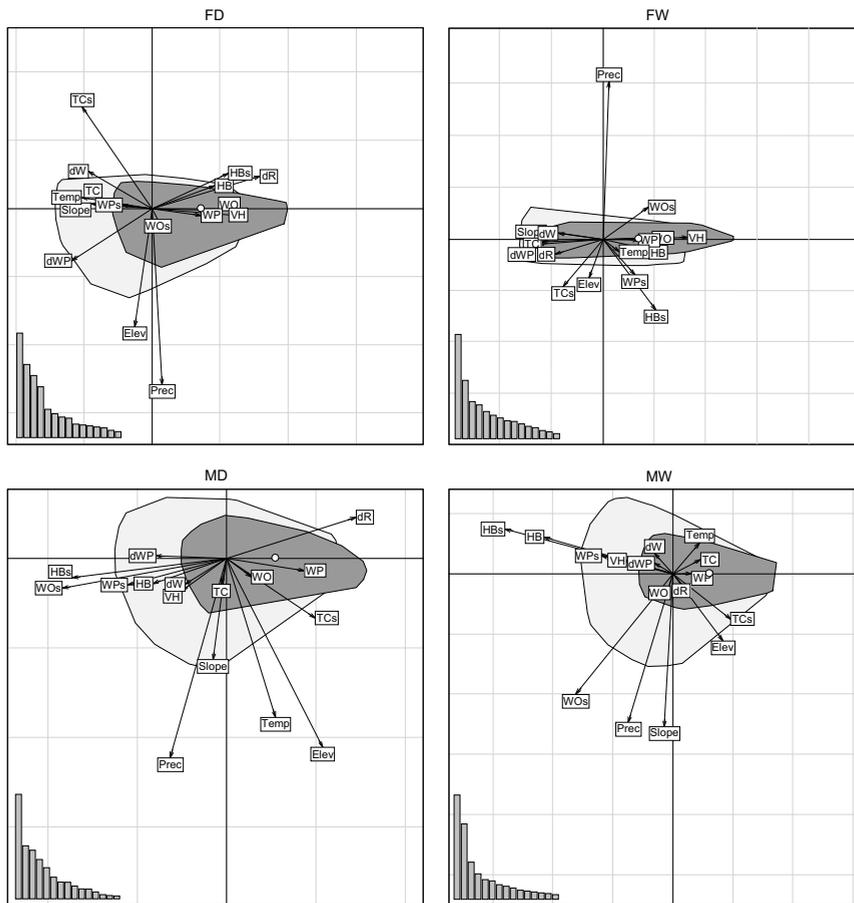
Figure 6.3: Ecological niche factor analysis (ENFA) bi-plots of female elephants in the dry season (FD), female elephants in the wet season (FW), male elephants in the dry season (MD) and male elephants in the wet season (MW). The plots display factorial maps of the used and available sites: the light grey area depicts the 95% minimum convex polygon (MCP) of the projection of the available sites in the subspace extracted by the ENFA, whereas the dark grey area depicts the 95% MCP of the projection of sites used by the elephants. The horizontal axis displays the first axis of the ENFA, i.e., the marginality axis, whereas the vertical axis represents the second axis of the ENFA, thus the first axis of specialization. The grey lines are separated by a distance of 0.25. The inset bar-plots show the contribution of each axis to the overall specialization. The vectors depict the correlations of the environmental variables with the two axes. For abbreviations of the environmental variables see Table 6.2. The white dot represents the centroid of the sites used by the elephants, while the origin of the plot is the centroid of the available sites.

Table 6.2: Coefficient values for each environmental variable on the first three axes of the ecological niche factor analysis: the marginality axis (M) and first two axes of specialization (respectively Sp1 and Sp2), for male and female elephants in the dry and wet season. HB: herbaceous biomass, TC: tree cover, WO: water occurrence, WP: water permanency, VH: vegetation heterogeneity, Elev: elevation, dW: distance to the nearest source of surface water, dR: distance to the nearest river, dWP: distance to the nearest water point, Temp: temperature and Prec: precipitation. The variables for which environmental context is explicitly considered are denoted with subscript s; see the footnotes for the distance (in km) at which environmental context was considered for each scenario (see Fig. 6.2).

	Female dry[a]			Female wet[b]			Male dry[c]			Male wet[d]		
	M	Sp1	Sp2	M	Sp1	Sp2	M	Sp1	Sp2	M	Sp1	Sp2
HB	0.25	0.09	-0.21	0.24	-0.05	-0.01	-0.21	-0.07	-0.34	-0.48	0.14	-0.03
HB_s	0.31	0.14	0.46	0.28	-0.37	-0.37	-0.44	-0.06	-0.09	-0.63	0.17	-0.27
TC	-0.21	0.03	0.06	-0.32	-0.01	0.00	-0.01	-0.07	-0.07	0.10	0.05	0.02
TC_s	-0.28	0.40	0.01	-0.21	-0.25	0.11	0.26	-0.17	-0.01	0.22	-0.17	0.07
WO	0.27	-0.01	-0.01	0.26	0.01	0.01	0.07	-0.05	0.00	-0.01	-0.04	-0.03
WO_s	0.02	-0.04	-0.25	0.24	0.17	-0.05	-0.47	-0.09	0.75	-0.36	-0.45	-0.13
WP	0.20	-0.03	-0.01	0.19	0.00	-0.01	0.22	-0.03	0.04	0.07	0.00	-0.03
WP_s	-0.12	0.01	-0.38	0.17	-0.19	0.10	-0.28	-0.08	-0.33	-0.27	0.07	0.12
VH	0.31	-0.03	-0.02	0.44	0.01	0.02	-0.13	-0.09	-0.15	-0.17	0.05	0.01
Elev	-0.07	-0.47	-0.57	-0.07	-0.20	0.09	0.28	-0.54	0.05	0.19	-0.25	-0.61
Slope	-0.24	0.02	0.06	-0.30	0.04	-0.12	-0.04	-0.29	0.17	-0.03	-0.57	-0.42
dW	-0.25	0.15	0.42	-0.24	0.03	-0.02	-0.12	-0.07	0.02	-0.07	0.08	0.01
dR	0.43	0.13	-0.11	-0.25	-0.08	-0.01	0.37	0.12	0.37	0.03	-0.04	0.03
dWP	-0.32	-0.21	-0.08	-0.34	-0.03	-0.03	-0.20	0.01	0.04	-0.07	0.04	-0.04
Prec	0.04	-0.70	0.05	0.03	0.83	0.71	-0.16	-0.57	0.06	-0.17	-0.55	0.46
Temp	-0.28	0.04	-0.01	0.08	-0.07	0.55	0.14	-0.46	-0.04	0.10	0.12	-0.34

[a]$HB_s = 31$, $TC_s = 40$, $WO_s = 32$, $WP_s = 30$
[b]$HB_s = 27$, $TC_s = 40$, $WO_s = 37$, $WP_s = 40$
[c]$HB_s = 13$, $TC_s = 11$, $WO_s = 18$, $WP_s = 15$
[d]$HB_s = 13$, $TC_s = 7$, $WO_s = 14$, $WP_s = 12$

environmental context. For HB and TC, including environmental context resulted in larger marginality coefficients, of the same sign, relative to non-spatial analyses. For WO and WP, however, the inclusion of environmental context resulted in smaller marginality coefficients for the females, but larger coefficients for the male elephants, yet of the opposite sign (Table 6.2). For all analysed scenarios the inclusion of environmental context increased the contribution of the corresponding environmental variables to the specialization axes (Table 6.2).

The ENFA analyses showed that the female elephants were primarily associated with areas with high water occurrence and permanency, herbaceous biomass and vegetation heterogeneity, areas close to water points or water in general (dWP and dW), and areas with low tree cover and gentle terrain (i.e., low slope; Fig. 6.3 and Table 6.2). Furthermore, the niche of the female elephants was most restricted in the dimension associated to elevation and precipitation. In contrast, the male elephants avoided areas with high herbaceous biomass, but preferred areas with high tree cover (Fig. 6.3 and Table 6.2). The elephants avoided areas associated with much surface water at a large scale (WO_s and WP_s). The niche of the male elephants was, like that of the female elephants, mostly restricted in those dimensions associated to elevation and precipitation, yet also to temperature and slope (Fig. 6.3). Both male and female elephants tended to be far from perennial rivers in the dry season (dR; Fig. 6.3 and Table 6.2), although they preferred

to be close to water points, or water regardless of the source (respectively dW and dWP). The effect of seasonality was very small compared to the effect of sexual segregation (Fig. 6.3).

Model predictability

The spatial models predicting HS performed very well for all scenarios (Fig. 6.4); all evaluation graphs increased monotonically (all $\rho > 0.95$), albeit in a non-linear fashion. The HS models were very robust, as the different cross-validation graphs exhibited low variance: the 95% confidence intervals were within 3% of the mean. Furthermore, the spatial models were able to differentiate HS for female elephants even at low HS values
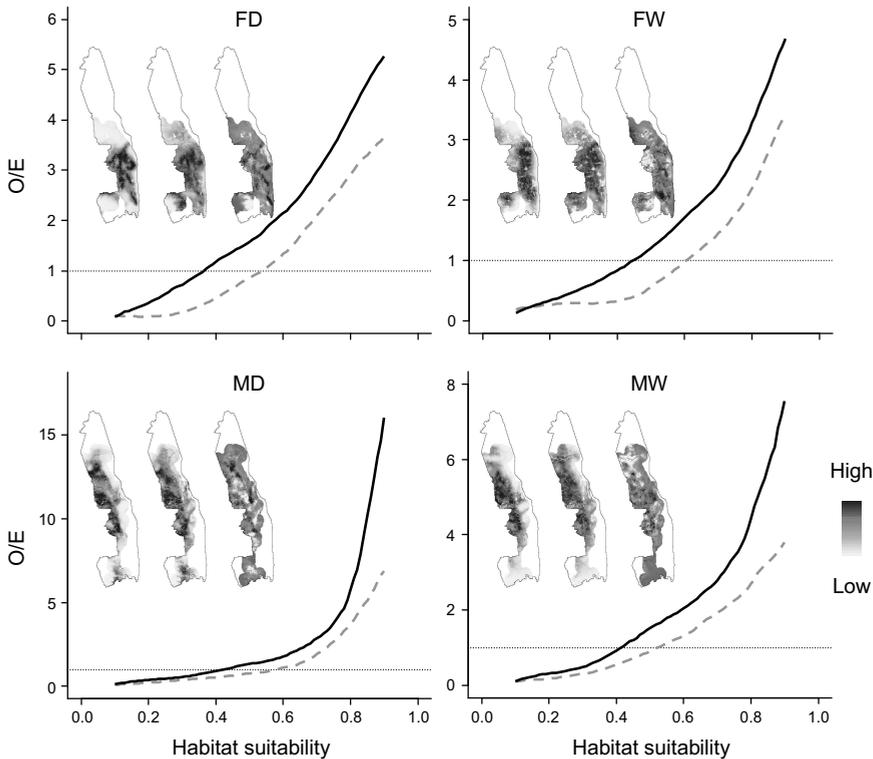
Figure 6.4: 10-fold cross validation graphs, showing the ratio between the observed number of evaluation points in each habitat suitability (HS) class (a moving window of size 0.2 centered around each value on the x-axis) relative to the expected number of evaluation points based on random chance (O/E), for female elephants in the dry season (FD), female elephants in the wet season (FW), male elephants in the dry season (MD) and male elephants in the wet season (MW). The solid black and dashed grey lines depict the mean O/E for over the 10 folds for the spatial models and non-spatial models, respectively. The confidence interval of the mean is within 3% of the mean, and therefore not displayed in this graphs. The dashed line at O/E = 1 indicates habitat use based on random chance. The inset maps represent the modelled HS using the spatial model (left map, with values from 0 to 1) and non-spatial model (middle map, with values from 0 to 1), and the difference between the two (right map: $HS_{spatial}$ - $HS_{non-spatial}$, with values from ca. -0.8 to ca. 0.5). Note that the models do not predict HS across the entire Kruger National Park, as only the area within 10 km from the recorded elephant locations was defined to be available to the elephants, and hence HS was predicted within this available area.

(< 0.4), whereas the non-spatial models were rather non-discriminatory at low HS values for the non-spatial O/E curves are non-increasing for low HS values. Moreover, the spatial models yielded higher O/E values for all scenarios than the non-spatial models, and thus were better able to differentiate between HS and randomness.

Discussion

Although the importance of spatial scale and spatial context when studying species distributions is increasingly being recognized (Wiens 2002; Wheatley & Johnson 2009), little is still known about the relative influence of localized and contextual environmental factors on the distribution of animals. We have therefore analysed the influence of environmental context, measured over an appreciable range of scales, on habitat selection by African elephants in Kruger National Park, South Africa. Our analyses highlighted the importance of explicitly considering environmental context at appropriate spatial scales for the analysis of habitat selection or the prediction of habitat suitability.

The scaling of environmental context

Our analyses showed that explicitly considering environmental context, in comparison to a non-spatial analysis, increased the quantified level of habitat selection by elephants, as measured by $\bar{D}^2$, M and S. Characteristic scales could be indicated for most analysed gradients, as nearly all gradients showed a distinct hump-shaped response with increasing buffer size. Our analyses support the view that the scaling of elephant-habitat relationships arises from the scale-dependent response of the elephants to their environment, instead of being determined by the spatial structure of the environmental variables themselves. Namely, the dominant scales of spatial variation regarding the examined environmental variables did not match the characteristic scales of the elephants' response to these environmental variables.

We believe that these characteristic scales of response are not determined by the perceptual range of the elephants, which could define an informational window on which decisions could be based (Olden *et al.* 2004), because it is impossible to visually assess the characteristics of the environment over all the scales that we considered. However, elephants have long-term, extensive spatial and temporal memory of acquired knowledge regarding their environment (McComb *et al.* 2001; Van Aarde *et al.* 2008; Van Langevelde & Prins 2008), and this could lead to informed decisions with regard to habitat selection, including the spatial scales at which they respond to their environment. The influence of memory on decision making by organisms has been implicated for a wide variety of species (e.g., Clayton & Dickinson 1998; Collett 2009; Wolf *et al.* 2009).

Scale-dependent habitat selection

Our analyses showed an example of what is often termed the "modifiable areal unit problem" or "change of support problem": relationships among variables at coarse scales are not necessarily of the same strength, or even direction, as those at fine scales (Openshaw & Taylor 1981; Gotway & Young 2002; Schabenberger & Gotway 2005; Wong 2009). Namely, the change in marginality coefficients when including the contextual influence of forage characteristics (HB and TC) showed a different pattern than when including spatial context regarding surface water availability (WO and WP). Whilst including environmental context increased the magnitude of the coefficients regarding HB and TC, it led to a reduction of the coefficients for WO and WP, or even to coefficients of the opposite sign.

Both sexes preferred areas associated with high local WO and WP, a pattern that was stronger in the dry season compared to the wet season. However, the male elephants avoided areas with a high availability of water at large scales, whereas the females did not show a distinct selection or avoidance of areas associated with abundant water at larger scales. Some caution is needed when explaining these findings. Instead of avoiding WO or WP at large spatial scales, it could be that the elephants were in fact not limited by water at larger scales. As Grant *et al.* (2008) argue, surface water can be expected to have a relatively small and localised effect in KNP, because water is usually widely available here. Because elephants drink on average every two days (Van Aarde *et al.* 2008), they need not always be in areas with a high availability of water, as long as they are effectively within walking distance from a source of water.

Our results are in contrast with the conclusions from Smit *et al.* (2007c) and Grant *et al.* (2008), who argued that the elephants in KNP are primarily associated with rivers and not with artificial water points. Namely, our results show that the elephants were predominantly located far from perennial rivers in the dry season, yet preferred areas close to artificial water points or water of any type. This indicates that the influence of artificial water points was over-riding the usual biological pattern, namely that elephants are found predominantly close to rivers, and suggests that the elephants were distributed across KNP in relation to the distance to the nearest water source, regardless of the surface-water origin. The marginality coefficients for overall distance to water were smaller than those for distance to water points, indicating that the influence of water points on the distribution of elephants might be stronger than the influence of rivers in the dry season. The influence of surface water on habitat selection by elephants has drawn much attention over the past years, as surface water management could possibly be used as a tool to influence the spatial distribution of elephants, thereby managing their impact on the vegetation (Chamaille-Jammes *et al.* 2007b,a; Smit *et al.* 2007a,c,b; Grant *et al.* 2008). Our results thus provide support for the notion that artificial surface water management is a highly promising, yet overlooked, tool for steering elephant distribution in KNP (Chamaille-Jammes *et al.* 2007b,a).

Given the ample supply of water in KNP, the elephants could thus select habitat based on other (limiting) resources, e.g., forage, but nevertheless be constrained by the distance to the nearest water source. The male elephants were found to select areas with high tree cover whilst avoiding areas with high herbaceous biomass, and increasingly did so at larger spatial scales. Conversely, the female elephants avoided areas with high tree cover while preferring areas with ample herbaceous vegetation, also showing more distinctive patterns of selection (or avoidance) when environmental context was explicitly considered. Thus, it could be that the elephants responded to their environment in a scale-dependent and hierarchical manner, with different environmental variables driving habitat selection at different spatial scales (Senft *et al.* 1987; Cushman & McGarigal 2002; Kristan 2006; Diez & Pulliam 2007). Our analyses suggest that the elephants first select areas in relation to vegetation characteristics at large spatial scales, and subsequently exhibit preferential habitat use regarding vegetation characteristics and surface water availability at finer scales. However, since our analyses were set up in a scale-dependent, yet not hierarchical, manner, we leave this as an untested hypothesis.

Sexual segregation in habitat selection

In line with other studies on sexual differences in foraging ecology of African elephants (Stokke 1999; Stokke & Du Toit 2000, 2002; Greyling 2004; Shannon *et al.* 2006b, 2010; Smit *et al.* 2007c), our analyses showed that the elephants exhibited sexual segregation regarding habitat selection. Sexual segregation in habitat selection is thought to be due to the smaller body size of the female compared to the male elephants, amplified by the fact that female elephants have a high reproductive input and live in permanent groups with close social bonding, resulting in high nutritional demands. On the other hand, male elephants are able to feed *in situ* for longer and utilise the more abundant but lower quality forage, as they do not experience the same social and energetic constraints as females (Shannon *et al.* 2006b).

Although Harris *et al.* (2008) observed sex-related elephant-vegetation associations in line with our findings, Smit *et al.* (2007c) found tree cover to be important for female elephants but not for male elephants, thereby contrasting our findings. This may be due to the limitations that the smaller female elephants and their youngsters may face in accessing the tree canopy, or because the male elephants target woody plants for reasons other than foraging, e.g., displacement behaviour (Shannon *et al.* 2006b). Besides their diverging response to vegetation, the male and female elephants also responded differently to terrain ruggedness. While the coefficients on the specialization axes were very low for the females regarding slope, the marginality coefficients indicate that the female elephants preferred areas associated to flat terrain, which is in line with the conclusion of Wall *et al.* (2006) that elephants avoid costly mountaineering. However, the marginality and specialization coefficients for the male elephants show that the male elephants were mainly found in areas with intermediate slope, yet avoided very flat or very steep areas. The preference of the male elephants for a more rugged terrain may be due to the establishment of nutrient hot-spots in a more undulating terrain (Nellemann *et al.* 2002; Grant & Scholes 2006), whereas the female elephants might be more limited in their mobility, which is amplified by youngsters at foot, and therefore prefer more gentle terrain.

Overall, the differences between the sexes was found to be larger than the differences between the seasons, providing further support for the notion that male and female elephants can effectively been seen as two distinct "ecological" species (e.g., Shannon *et al.* 2006b).

Model predictability

Our analyses showed that explicitly incorporating environmental context at appropriate spatial scales can lead to a major increase in the predictive ability of habitat suitability models, thereby being beneficial for scientific purposes, as well as management and conservation initiatives. Including environmental context in habitat suitability models of elephants in our study area resulted in more significant and consistent models than non-spatial models that ignored the influence of environmental context. The spatial models yielded higher O/E scores, thereby being better able to discriminate between habitat suitability and randomness. Moreover, the spatial models yielded more consistent monotonically increasing cross-validation curves, meaning that they were better able to predict habitat suitability with higher classification resolution (Hirzel *et al.* 2006). Furthermore, the models had a high stability, as they exhibited little cross-validation variance, probably due to the large size of our dataset (Guisan & Thuiller 2005).

Implications for ecological studies

Being able to accurately assess the relationships between organisms and their environment, or predict the suitability of habitat for a specific species at any point in space is an important prerequisite for effective management and conservation of natural systems (Boyce *et al.* 2002; Guisan & Thuiller 2005; Guisan *et al.* 2006; Hirzel *et al.* 2006; Thorn *et al.* 2009). However, the effects of spatial scale on model performance and predictability are amongst some of the most prominent challenges to habitat selection analysis and species distribution modelling (Araújo & Guisan 2006). Our analyses highlighted the importance of explicitly considering the influence of environmental context on habitat selection, and especially the spatial scale at which environmental context exerts influence on the patterns of habitat use by organisms. We have thus shown the importance of choosing the scale of analyses when studying species-environment relationships, and demonstrated a method to assess the importance of environmental context measured along an appreciable range of scales. However, the scale of analysis is often chosen arbitrarily, because it is convenient or dictated by the scale of available data products (Rushton *et al.* 2004; Meyer 2007). As advances in satellite imagery and remote sensing permit scientists to access spatial data at increasingly higher resolutions (Gotway & Young 2002; Mayer & Cameron 2003), the relative influence of environmental context in analyses of species distributions may become increasingly important. We conclude that ecologists should explicitly consider the influence of environmental context, at appropriate spatial scales, in their analyses, as this is paramount to understanding the processes behind the distribution of organisms, and required for successful ecosystem management.

7

Beyond the here and now: herbivore ecology in a spatial-temporal context

*T*he fascinating question of how organisms are distributed in space and time has inspired many studies, including those presented in the previous chapters, to seek explanations. It is the very foundation of ecology as a scientific discipline, since it is the study of the interactions that determine the distribution and abundance of organisms (Krebs 2008). Hence, ecology deals with how individuals are affected by, and how they affect, their biotic and abiotic environment (Begon *et al.* 1996; Turchin 1998; Currie 2007; Elith & Leathwick 2009). A myriad of processes, operating over a wide range of spatial and temporal scales as well as organizational levels, determine the relationships between organisms and their environment, posing formidable challenges to identifying the key processes shaping species-environment relationships at different spatial and temporal scales (Levin 1992; Wu & Li 2006).

As a primary mechanism coupling species to their environment, movement of individual organisms is a fundamental characteristic of life (Turchin 1998; Bergman *et al.* 2000; Nathan 2008). It is the glue that sticks ecological processes together (Turchin 1996), because it plays a major role in determining the fate of individuals, ultimately leading to the spatial structure and dynamics of populations (Turchin 1991; Nathan 2008). Hence, studying the detailed patterns of organismal movement or studying the broad-scale population distribution patterns is essentially studying similar things albeit at different scales (Lima & Zollner 1996). Because of their crucial role in almost any ecological and evolutionary process, the patterns of organismal movement and the distribution patterns of

populations have received much theoretical and empirical attention in ecology over the past decades (Patterson *et al.* 2008; Schick *et al.* 2008). Yet, identifying the effects of environmental heterogeneity on the movement and distribution of organisms, and translating observations taken at small spatial and temporal scales into expected patterns at broad scales are major challenges that remain (Morales & Ellner 2002; Nathan 2008; Romero *et al.* 2009).

In this thesis, I have presented several studies framed around species-environment relationships, with a focus on terrestrial mammalian herbivores. Using theoretical modelling as well as analyses of field data, I studied species-environment relationships over a broad array of scales: from short-term and small-scale movement responses of African elephants (*Loxodonta africana*) to environmental heterogeneity (Chapter 2), to the influence of environmental characteristics on their long-term and large-scale population distribution patterns (Chapter 6).

Themes covered in this thesis

Albeit with some overlap, these studies can be classified into the following overarching themes:

1. organismal movement in relation to environmental heterogeneity (Chapter 2);

2. temporal variation in species-environment relationships (Chapter 2, 4 & 6);

3. feedbacks between organisms and their food resources (Chapter 3 & 4);

4. the influence of memory on organismal movement (Chapter 4);

5. species-specific scales of response to environmental heterogeneity (Chapter 5 & 6).

Below, I discuss these themes separately, after which I focus on the prominent issue throughout the entire thesis, namely the importance of the scale-dependency and context-dependency of species-environment relationships. I discuss the importance of considering the above-mentioned themes separately, but also the need to study them *in toto* if one aims at increasing the understanding of the mechanisms behind observed spatial-temporal ecological patterns.

Organismal movement in relation to environmental heterogeneity

Terrestrial herbivores are faced with spatial variation in the abundance and quality of food resources, either continuously (e.g., grazers feeding on a continuous layer of herbaceous vegetation) or patchily (e.g., browsers feeding on a discontinuous layer of trees and shrubs) distributed in space. Even in an otherwise completely homogenous environment, spatial variation in the abundance of food resources influences the short-term movements of organisms (De Knegt *et al.* 2007). Generally, when animals are in an environment with ample food resources, they adopt a more tortuous movement strategy by turning more frequently or with larger turns ("klinokinesis") while reducing their step size or locomotory speed ("orthokinesis") compared to an environment with only few resources (Benhamou & Bovet 1989; Crist *et al.* 1992; McIntyre & Wiens 1999a; Viswanathan *et al.* 1999; Goodwin & Fahrig 2002; Bartumeus *et al.* 2003, 2005; De Knegt *et al.* 2007; Barraquand & Benhamou 2008). This causes less displacement and a more thorough coverage of profitable places (i.e., areas with high resource density), yet faster transit in poor environments and thus a higher chance of finding new, perhaps better environments (Senft *et al.* 1987; De Knegt *et al.* 2007).

Moreover, animals typically spend more time foraging on resources that are more profitable (Charnov 1976; Bailey & Provenza 2008; Hengeveld *et al.* 2009). Combined with an adjustment of its movement pattern, this raises an herbivore's efficiency of resource utilization with increasing resource density (De Knegt *et al.* 2007). Over longer time frames, the spatial distribution of food resources thus leads to varying population densities in space (Patlak 1953; Senft *et al.* 1987; Turchin 1991). Studying the influence of resource density on the movements by organisms can therefore serve as an important step toward identifying the mechanisms behind the spatial distribution of organisms (Turchin 1991; Morales & Ellner 2002; Del Mar Delgado & Penteriani 2008; Romero *et al.* 2009). However, attempts to translate the small-scale movement patterns of individuals into patterns of population distribution using information on resource density alone (e.g., using diffusion approximation; Patlak 1953; Turchin 1991, 1998) have had varying success (Turchin 1991; Morales & Ellner 2002), for reasons I will discuss below.

Before getting too far into the consideration of how environmental heterogeneity influences the movements and distribution of organisms, it is first necessary to understand how and why the landscape is heterogeneous (White & Brown 2005). Generally, the initial conditions for environmental heterogeneity are set by spatial variation in abiotic conditions, as shaped by climate, geology, and topography (Mackey & Lindenmayer 2001; Turner *et al.* 2001; White & Brown 2005). Climate acts as a strong control on biogeographic patterns through the distribution of energy and water, the effects of which are modified by the geologic processes of tectonics and erosion producing patterns of the physical relief and soil development (Turner *et al.* 2001). These processes have created a crumpled, dimpled, and layered land surface, which interacts with the predictable patterns of solar energy input, air and water pressure, tidal exposure, and other factors to create an abiotic, physical template on which the biota of a region develop (Turner *et al.* 2001; White & Brown 2005).

This template exerts influence on organisms in various ways. Because it affects the flow of many quantities, including organisms, propagules, energy and matter through a landscape, it creates spatial and temporal variation in (1) the resources that organisms require, e.g., mineral nutrients and water, and (2) the environmental conditions that influence the physiology of organisms, e.g., temperature and air/water pressure (Mackey & Lindenmayer 2001; Turner *et al.* 2001; White & Brown 2005). Because of its generally high correlation with key components of the abiotic template, it has been argued that altitudinal gradients are among the most powerful "natural experiments" for testing ecological responses of organisms to the physical template (Korner 2007). Altitudinal gradients comprehensively represent, both directly and indirectly, a combination of different gradients regarding resources and environmental conditions in a simple way (Austin 2002; Korner 2007; Legendre *et al.* 2009).

However, there are two categories of gradients related to altitude, the confounding of which has introduced confusion in the scientific literature on altitude phenomena (Korner 2007). These categories of altitude-related gradients include (1) those physically tied to meters above sea level, such as atmospheric pressure, temperature and (depending on the region) rainfall; and (2) those that are not generally altitude specific, but dependent on derivatives (e.g., slope, aspect, relative topographic position) of altitudinal gradients, e.g., soil moisture, hours of sunshine, wind and geology (Karr & Freemark 1983; Korner 2007; Elith & Leathwick 2009).

Altitude-related gradients

Through correlating with more functionally relevant predictors such as temperature, rainfall and solar radiation, altitude influences both animal physiology and the productivity and structure of vegetation upon which animals depend for shelter and nutrients (Karr & Freemark 1983; Mackey & Lindenmayer 2001; Austin 2002; White & Brown 2005; Korner 2007; Elith & Leathwick 2009). In aquatic systems, depth is an indirect proxy for several proximal predictors: temperature and its variability, salinity, light, pressure, and the availability of elements (Elith & Leathwick 2009). These influences are most apparent at broad spatial scales, generating relatively continuous variation in resource availability and environmental conditions over substantial distances, resulting in spatially varying population densities (White & Brown 2005).

Movement by large herbivores along an altitudinal gradient may thus be a strategy to cope with changing temperatures, enhance access to areas of high food abundance or quality, and reduce the risk of predation (Fryxell & Sinclair 1988; Mysterud 1999). For example, cervid species (*Cervidae*) in temperate regions typically move to higher elevation during the summer and to lower elevation during the winter (Mysterud 1999, and references therein). There is general agreement that their migration in winter to low altitudes is a strategy to find areas with shallow snow depth, what increases their access to forage, decreases their costs of locomotion and makes them less vulnerable to predation (Fryxell & Sinclair 1988; Mysterud 1999). Moreover, the conditions for thermoregulation are more favourable at lower elevations with generally higher temperatures (Mysterud 1999). The mechanism explaining their migration to higher elevations in spring and summer is, however, less clear, although it might be that they obtain a diet of higher quality there (Fryxell & Sinclair 1988).

Similar findings are reported by Wang (2009), who showed that the driving force behind the altitudinal migration of giant pandas (*Ailuropoda melanoleuca*) and golden takins (*Budorcas taxicolor bedfordi*; see also Zeng *et al.* 2008) in the Qinling Mountains, China, is the result of seasonal and altitudinal variation in plant phenology. Moreover, Ngene *et al.* (2009) found African elephants in the Marsabit Protected Area, Kenya, to move to the higher elevation mountain forest during the dry season, possibly because it provides the only drinking water during the dry season, yet to move to the lowlands during the wet season.

Not strictly altitude-related gradients

Whilst the influence of such broad altitude-related gradients on the movements and distribution of organisms is generally acknowledged, it is much less widely acknowledged that on a smaller scale there can be a great deal of variation indirectly related to altitude (Begon *et al.* 1996). As one "zooms in" to smaller scales within altitudinal gradients, additional processes become dominant, and the continuous gradient pattern becomes swamped by the now dominant local processes (White & Brown 2005). For example, temperature does not vary smoothly and monotonically with elevation when examined in detail on sufficiently small scales (White & Brown 2005). At fine spatial scales, the influence of topographical indices such as slope angle, aspect and relative topographic position become important. At fine scales, the heterogeneity of the physical template interacts with climatic variables to redistribute the availability of resources (e.g., moisture and nutrients) and influence the environmental conditions (e.g., temperature and solar radiation) in ways that have important consequences for ecological processes (Chapter

2; Kumar *et al.* 1997; Turner *et al.* 2001; Caylor & Shugart 2006).

For example, slope angle may directly affect the movement of organisms by imposing considerable energetic costs on travel (Wall *et al.* 2006), or by constraining their movements (either permanently when slopes are to steep, or temporarily, e.g., during wet periods when hillslopes become slippery: Ngene *et al.* 2009). Indirectly, altitude-related topographical indices influence species-environment relationships by influencing the distribtuion of heat, water and nutrients through a landscape. For example, the sinking of dense, cold air into the bottom of a valley at night (cold-air drainage) can make the valley bottom many degrees colder than the hillslope or crest; and the sun shining on a south-facing slope (on the northern hemisphere) can make it many degrees warmer than the rest of the landscape (Begon *et al.* 1996; Venter *et al.* 2003; Pypker *et al.* 2007). More-over, on hillslopes, the topographical influence on water flow is a driving force behind soil differentiation, leading to gradients of increasing soil moisture and nutrients content from the top of a catena to the bottom of a valley, thereby having severe consequences for vegetation patterning and ecosystem processes (Milne 1936; Chamran *et al.* 2002; Shorrocks 2007; Hartshorn *et al.* 2009).

These topographically mediated soil moisture and nutrient gradients are maximized under a semi-arid climate and in areas with gentle slopes, conditions characteristic for most African savanna systems (Venter *et al.* 2003; Hartshorn *et al.* 2009). The extreme differentiation of African catenas often coincides with nutrient-poor and open vegetation on the upslope soils, and nutrient-rich and dense vegetation on the downslope soils (Hartshorn *et al.* 2009). Hence, considering the influence of topographically mediated patterns in vegetation on the patterns of space-use by animals, through its influence on the spatial variation in the abundance and quality of food resources, as well as possibilities for shelter and thermal cover, are paramount to understanding the patterns of habitat selection by African elephants (Chapter 2). However, the influences of hillslope drainage of moisture and nutrients are not confined to savanna systems. For example, in arctic regions, a southerly exposition and good moisture drainage on hillslopes and ridges increases the chance of finding permafrost at deeper soil depth, and thus represents favourable conditions for the excavation of a den, as demonstrated by Szor *et al.* (2008) for arctic foxes (*Alopex lagopus*) on Bylot Island, Canada.

Thus, attention need not be confined to raw altitudinal gradients when seeking to understand the relationships between organisms and the abiotic, physical template, because important ecological drivers related to local derivatives of elevation are then likely to be overlooked (Chapter 2; Begon *et al.* 1996; Korner 2007). Hence, identifying the causal driving mechanisms related to altitude and topographical position ensures that a study moves beyond describing structure or pattern to include the functional role of altitudinal gradients (Pickett *et al.* 2003). This has proven to be invaluable for understanding the relationships between organisms and their environment in ecosystems ranging from savannas (Chapter 2; Nellemann *et al.* 2002), arctic tundra (Szor *et al.* 2008) to the tropics (Karr & Freemark 1983), and with parallels in aquatic systems (e.g., Vilchis *et al.* 2006; Schofield *et al.* 2009).

Temporal variation in species-environment relationships

Thus, taken together, the interactions of the physical template with its associated vegetation pattern produce the underlying spatial context for animals and define the set of prevailing environmental conditions that impinge upon, or are available to, an animal

(Mackey & Lindenmayer 2001; Turner *et al.* 2001; White & Brown 2005). However, no environment is constant over time, hence no behaviour of an organism can match a changing environment unless it too changes (Begon *et al.* 1996). Among the prominent temporal environmental changes are the rhythmic cycles of the seasons, the movements of the tides and the circadian cycles of solar energy input (Begon *et al.* 1996). Such cyclic changes result in temporarily varying environmental conditions (e.g., seasonality in temperature and rainfall, and diurnal patterns of solar radiation and temperature); patterns that interact with the spatial heterogeneity of the biotic and abiotic template to influence the relationships between organisms and their environment (Chapter 2).

For example, in Chapter 2 I showed that the seasonal pattern of terrain-use by elephants in Kruger National Park (KNP), South Africa, is likely driven by the seasonal pattern of rainfall, which influences the quality and quantity of available forage, with a higher quality of forage for longer periods in the low-lying parts of the landscape (i.e., valleys). This seasonally varying influence of local topography has been demonstrated for both grazing and browsing animals (Bell 1971; Nellemann *et al.* 2002; Du Toit 2003). Other examples of seasonal cycles of migration by animals along altitudinal gradients have been discussed above (i.e., Fryxell & Sinclair 1988; Mysterud 1999; Zeng *et al.* 2008; Ngene *et al.* 2009; Wang 2009), and similar patterns are found in the seasonal movements of people with their livestock, typically to higher pastures in summer and to lower valleys in winter (i.e., "transhumance"; Senft *et al.* 1987).

At shorter, diel time scales, organisms may choose to lie in the sun, or hide in the shade, as they may experience a baking midday sun and a freezing night (Begon *et al.* 1996). In Chapter 2, I showed that the daily patterns of terrain-use by elephants in KNP are most probably governed by thermoregulatory behaviour due to circadian rhythms of temperature and solar radiation, stimulating the elephants to seek shade under the denser canopy of the vegetation in the valleys during times of peak temperature, i.e., midday. Thus, the spatial and temporal context regarding environmental conditions interact to create the observed spatial-temporal patterns of herbivore distribution.

Besides the seasonal and circadian rhythms in the distribution patterns of organisms (Chapter 2), organisms may alter their movements in response to an increasing experience with a previously unknown environment (De Knegt *et al.* 2007). Moreover, organismal movement may change over time due to a change in the accessibility of the terrain or because resources become buried by snow (Senft *et al.* 1987; Fryxell & Sinclair 1988; Mysterud 1999; Ager *et al.* 2003; Fortin & Melles 2009; Ngene *et al.* 2009; Wang 2009); an increased importance of dominance relationships during times of resource scarcity (Wittemyer *et al.* 2007); temporal changes in perceived predation risk (Brown 1988; Gibson *et al.* 1998; Frair *et al.* 2005); variation in the level of satiation (McIntyre & Wiens 1999b); or the birth of young individuals that limit the movements of herds.

Hence, a major challenge for the successful upscaling of short-term movement patterns into long-term population distribution patterns thus resides in the complexity of temporarily changing movement behaviour (Morales & Ellner 2002; Fryxell *et al.* 2008; Patterson *et al.* 2009). These temporal changes in movement behaviour may be the reason why the use of short-term movement patterns in an attempt to predict the long-term pattern of population distribution has led to varying results (Morales & Ellner 2002; Del Mar Delgado & Penteriani 2008; Nathan 2008; Patterson *et al.* 2008; Gurarie *et al.* 2009). As animals change their movement behaviour facultatively in relation of variations in internal state (e.g., heat stress, hunger) and environmental conditions (e.g., temperature,

resource abundance and quality), temporal changes in movement and behaviour need to be understood and taken into account (Morales & Ellner 2002; Fryxell *et al.* 2008; Nathan 2008; Patterson *et al.* 2008; Bartumeus 2009; Gurarie *et al.* 2009).

Herbivore-vegetation feedbacks

Besides temporarily changing herbivore behaviour, a potentially complicating issue when studying species-environment relationships arises when food resources not only have an unidirectional influence on herbivores (i.e., if herbivores only *react to* environmental heterogeneity), but when food resources have reciprocal linkages with the herbivores feeding upon them (i.e., when herbivores *react to* and *create* environmental heterogeneity; Chapter 3). Large herbivores have the potential to modify the architecture, physiology, biochemistry, productivity and phenology of the plants they feed on (Chapter 3; Laws 1970; Du Toit *et al.* 1990; Agrawal 1998; Nunez-Farfan *et al.* 2007; Skarpe & Hester 2008). Thus, a "feeding loop" can develop, where animals induce changes in plant morphology and/or physiology, leading to further herbivory and further changes in the plants (Chapter 3; Makhabu *et al.* 2006). Such a feedback loop is called "self-facilitation" in Chapter 3, since it is advantageous for the herbivore creating it; however, it may also facilitate foraging by other species (Makhabu *et al.* 2006; Kerley *et al.* 2008).

That organisms actively modify their environment and influence that of other species is not a particularly novel observation: organisms have been modifying their environment since the first microbial consortia over 3 billion years ago began trapping and binding sediment, altering their physical and geochemical environment and producing stromatolites and, eventually, the first reefs (Erwin 2008). Organisms that are noted as key sources of environmental heterogeneity have been recognized as "ecosystem engineers" (Jones *et al.* 1994, 1997). Although there are environments in which there is a predominant engineer that builds major structure in the environment (e.g., elephants or termites), almost all environments are physically engineered by numerous organisms at different scales, in different ways, and with different consequences (Pickett *et al.* 2003).

Examples include the well-known "grazing lawn" phenomenon where ungulate grazers are able to maintain permanent grazing lawns through a positive feedback loop (grazing-regrowth-regrazing) that generates enhanced productivity from a short sward (Chapter 3; McNaughton 1984). Famous examples of grazing lawns are found in the Serengeti and other African systems, maintained by a variety of grazing ungulates, and grasslands in North American maintained by bison (*Bison bison*). Furthermore, Van der Wal *et al.* (2000) reported that brown hares (*Lepus europaeus*) facilitated grazing by brent geese (*Brenta bernicla*) in salt marshes in the Netherlands by preventing regrowth of the shrub *Atriplex portulacoides*. Recently, Colman *et al.* (2009) showed that grazing reindeer (*Rangifer tarandus*) in Norway avoided pastures no longer in use by sheep (*Ovis aries*), likely due to senescent plant material, but preferred pastures with intermediate sheep grazing, or, to a lesser extent, pastures that were mown.

While such herbivore-vegetation feedbacks relate to a two-dimensional, one-layered herbaceous vegetation structure, the three-dimensional influence of browsing on vegetation may be more complex (Du Toit *et al.* 1990; Makhabu *et al.* 2006). Recent investigations regarding the interactions between woody vegetation and browsing herbivores have shown that repeated browsing may alter the vertical architecture of trees, the quality of leafs and shoots, or the density of shoots within the canopy (Chapter 3; Makhabu *et al.* 2006; Fornara & Toit 2007; Kerley *et al.* 2008; Skarpe & Hester 2008; Kohi *et al.*

2010). The reduced height of browsed trees leads to a larger proportion of shoots and leaves remaining available within browsing height, and the improved accessibility, together with the larger size and generally higher nutritional value of regrowth shoots, increases the probability of browsing a previously browsed plant (Chapter 3; Fornara & Toit 2007; Skarpe & Hester 2008). However, not only large browsing herbivores may alter the architecture of woody plants, also small insects like gall-forming aphids (*Baizongia pistaciae*) have been found to modify the architecture of trees (Kurzfeld-Zexer *et al.* 2010).

Repeated browsing may keep the woody vegetation in a hedged state, resulting in "browsing lawns" resembling the grazing lawns discussed above (Chapter 3; Fornara & Toit 2007). Moreover, it may prevent the successful regeneration of shrub and tree species. These browse-browser interactions have potentially severe consequences for ecosystem functioning. For example, Prins & Van der Jeugd (1993) showed the influence of a drastically reduced size of herbivore populations (e.g., due to poaching or anthrax epidemics), and the conditions for seedling establishment and bush encroachment. Furthermore, the trophic cascade involving wolves (*Canis lupus*), elk (*Cervus elaphus*), and aspen (*Populus tremuloides*) in Yellowstone National Park, USA, recently resulted in the first significant growth of aspen in over half a century, after wolves were reintroduced to the park in 1995-1996 (Ripple & Beschta 2007). The reintroduction of the wolves had reintroduced a "landscape of fear", what changed the spatial distribution of the elk, so that the aspen are now returning in some areas that are currently being avoided by the elk, yet where elk previously suppressed their regeneration. Similar findings by Ripple & Beschta (2008) in Yosemite National Park, USA, concerned trophic cascades involving cougar (*Puma concolor*), mule deer (*Odocoileus hemionus*), and black oaks (*Quercus kelloggii*). Moreover, a combination of climate, fire, elephants and human impact has been cited as a major cause to the almost complete extinction of woodland in Amboseli National Park, Kenya, since 1950; however, experiments showed that elephants alone were sufficient to prevent woodland recovery (Western & Maitumo 2004).

These examples highlight the importance of herbivore-vegetation feedbacks, and spatial variation therein, on the functioning of ecosystems. Even in the absence of underlying spatial environmental heterogeneity, positive herbivore-vegetation feedbacks can lead to reciprocal spatial patterns in vegetation and herbivory (Chapter 3). Herbivores create spatial heterogeneity with every step they make and bite they take (Owen-Smith 2002). This may initiate a positive feedback even in completely homogenous space. Since herbivores respond to their environment (or influence their environment) in a spatially explicit manner, these feedback loops can lead to large-scale patterns in vegetation and herbivory (Chapter 3). Such biologically generated heterogeneity layers on top of the heterogeneity of a physical template (Pickett *et al.* 2003; White & Brown 2005), in ways that increase or nullify the spatial patterns initially present. The role of herbivores in increasing or decreasing environmental heterogeneity depends on the density of herbivory: intermediate herbivore densities lead to an increased heterogeneity, while high herbivore densities lead spatial homogenization (Chapter 3; Adler *et al.* 2001).

The influence of memory on movement

Furthermore, the use of memory by organisms can be a major impediment to the successful upscaling of short-term movement patterns into long-term distribution patterns. While many studies regarding the movement patterns of organisms are based on premises

from simple statistical mechanical theory for memory-free, random-walk and diffusion processes, animals from many taxa generally express strategic home range behaviour and site fidelity, thereby directly violating the primary model assumptions (Davis & Stamps 2004; Gautestad & Mysterud 2005; Börger *et al.* 2008). The importance of spatial familiarity for the movements and patterns of habitat selection by animals can have multiple origins, including territoriality, nathal philopatry or home ranging behaviour (Davis & Stamps 2004; Börger *et al.* 2008), spatial neophobia (Wolf *et al.* 2009) or positive plant-herbivore feedbacks (Chapter 3; Colman *et al.* 2009; Wolf *et al.* 2009). Furthermore, spatial familiarity may lead to frequent visits to sites with limiting resources.

In all cases, memory plays an important role, and it is invoked whenever an animal initiates a directed displacement toward a target beyond its instant field of perception (e.g., smell, sound, and sight; Gautestad & Mysterud 2005). Memory is thought to play an important role for organisms in landscapes with little resource variability, since an individual's previous moves are then important sources of information for decisions about future movement (Mueller & Fagan 2008; Collett 2009). Memory enhances the efficiency with which animals can exploit their resources, as it makes it easier to return to places and things that are useful, and to avoid those that may be dangerous or costly (Collett 2009).

For example, in Chapter 4 I have shown that elephants frequently re-visited previously visited sites, even after long periods. The elephants did not avoid previously utilized areas but seemed to exhibit the tendency to return to sites already visited above what can be expected from random movements alone. The patterns of site revisitation were related to the proximity to surface water and vegetation cover, mediated by seasonality in rainfall: the elephants were more likely to be site-faithful when surface water became scarce (dry season) and in areas close to water, and they were less site-fiathful in areas with a high tree cover. However, female elephants revisited sites close to water and with high tree cover more often, probably because these areas provide not only water, but also shelter and abundant forage that is of high quality. Fryxell *et al.* (2008) showed that free-ranging elk in southern Ontario, Canada, tended to frequently revisit sites where local residents provided hay. Given that memory can play a demonstrable role in determining animal movement patterns, it needs to be accounted for in analyses of movement and habitat selection by organisms.

Species-specific scales of response to their environment

Important concepts relating to scale arise when the relationships between organisms and their environment are considered (Chapter 5 and 6; Wiens 1989; Levin 1992; Turner *et al.* 2001). Namely, a beetle does not relate to its environment on the same scales as a vulture, even though both are scavengers, and a plant eating insect most likely experiences its environment at different scales than does a large herbivorous mammal like the elephant (Turner *et al.* 2001; Manning *et al.* 2004). Each individual organism has an idiosyncratic view of the world as function of its own physical and cognitive attributes and its exposure to environmental variation (Mac Nally 2005). Such attributes may include the body mass, sensory capabilities (visual, aural), memory, and mobility of organisms (e.g., Addicott *et al.* 1987; Lima & Zollner 1996). Thus, there is a strong imperative to focus on the scales that are appropriate for the organism, recognizing that our human-based perception of scale and pattern may not be the right one: just because a particular scale seems "right" to us is no assurance that they are appropriate to reef

fish, barnacles, birds or elephants (Wiens 1989; Turner *et al.* 2001).

Scale is usually defined in terms of the spatial or temporal dimensions of an object or process, characterized by both grain and extent (Dungan *et al.* 2002; Schneider 2001). Ideally, the extent and grain of analysis are selected based on relevant information regarding a species' biology (Wheatley & Johnson 2009). For example, the extent may be determined by the extent of a home range or the field of view for birds flying at high altitude, and the grain may be set by the detail at which organisms perceive their environment or base their decisions upon. However, this kind of information is often unknown, especially when it concerns the grain of perception and decision making by organisms (Wiens 1989; Holland *et al.* 2004; Wheatley & Johnson 2009). The scales of analysis or modelling are therefore often selected not based on the relevance for the ecological phenomenon under study, but based on data availability, convenience, or our human perception of the system (Mayer & Cameron 2003; Dormann 2007; Wheatley & Johnson 2009). Hence, scale mismatches are to be expected, and it is therefore important to understand the way analyses are affected by the use of data at inappropriate scales (Gotway & Young 2002). Much research has therefore recently been conducted on the scaling of species-environment relationships, given the constraints set by the extent and grain of available data (e.g., Chapter 5 and 6; Steffan-Dewenter *et al.* 2002; Cushman & McGarigal 2004; Holland *et al.* 2004; Mayor *et al.* 2007).

Such studies demonstrate that if one studies a system at an inappropriate scale, one may not detect its actual dynamics, but may instead identify patterns that are artefacts of scale (Wiens 1989). Hence, conclusions about a phenomenon based on a set of observations at the wrong scale may misconstrue the importance of environmental factors thought to drive system behaviour (Chapter 5; Cushman & McGarigal 2004; Wheatley & Johnson 2009). In the fields of geography and spatial statistics, such scale effects have been studied for several decades in the context of the "modifiable areal unit problem", "change of support problem" or "ecological fallacy" (e.g., Openshaw & Taylor 1981; Gotway & Young 2002; Wong 2009). It led Openshaw & Taylor (1979) to conclude that there are "a million or so correlation coefficients" for analyses at different scales yet for the same study system.

In Chapter 5, I come to a similar conclusion, since I show that the regression coefficients and the proportion of variance explained by environmental variables vary as function of the scale of analysis, with a reduced portion of variance explained by environmental predictors, and with invalid significance estimates and biased regression coefficients in case of a scale mismatch. This stems from the non-zero covariance between regressor and error term stemming from the correlation between local and contextual information regarding environmental predictors, or from the spatial smoothing of data (Chapter 5). This leads to the violation of one of the assumptions of regression analyses, and henceforth faulty conclusions (Ebbes *et al.* 2005; Luskin 2008). Moreover, I show in Chapter 5 that a scale mismatch leads to residual spatial autocorrelation (RSA), an issue that has received considerable attention over the past years (e.g., Lennon 2000; Diniz-Filho *et al.* 2003; Beale *et al.* 2007; Dormann *et al.* 2007; Hawkins *et al.* 2007; Bini *et al.* 2009), and has led to the development of various spatial regression techniques devised to deal with the effects of RSA. However, I show that such techniques should not be used as a quick fix for modelling spatial data in case of a scale mismatch: when the species-environment relationships are scale-dependent and if this is not incorporated in the analysis, this may be a more severe threat to the interpretation of ecological phenom-

ena than an inflated Type I error due to RSA (Chapter 5; Haining 2003; Wagner 2004; Van Teeffelen & Ovaskainen 2007).

In Chapter 6, I study the spatial scaling of elephant-environment relationships in KNP, and show that the scale used for analysis or prediction has a major influence on the observed patterns of habitat selectivity or predictability of habitat suitability. The results of Chapter 6 indicate that the elephants preferred areas associated to high local water availability, a pattern that was stronger in the dry season compared to the wet season. However, this pattern changed as function of the scale of analysis, even to the extent that elephants seemed to avoid areas with a high availability of water at large scales. However, as argued in Chapter 6, instead of avoiding areas with a high water availability at large spatial scales, it could be that the elephants were in fact not limited by water at larger scales (water is widely available in KNP), and hence could select habitat based on other (limiting) resources, e.g., forage. This conclusion is consistent with other findings reported in Chapter 6, namely that the influence of vegetation characteristics on the distribution of elephants increased with increasing spatial scale of analysis.

Thus, these chapters (5 and 6), and the studies by other authors (e.g., Steffan-Dewenter *et al.* 2002; Cushman & McGarigal 2004; Holland *et al.* 2004; Mayor *et al.* 2007; Schmidt *et al.* 2008) highlight that species-environment relationships are scale-dependent, wich has severe consequences for the estimation of the significance and strength of these relationships. Moreover, they show that different environmental predictors may be important at different spatial scales, depending on the spatial patterns in the environment and the biology of species. Since scale mismatches are a serious impediment to the understanding of species-environment relationships, they are to be avoided by analysing data at appropriate spatial scales. The key to achieving this is in shedding our own conceptions of environmental scale and instead concentrating on the perceptions of the organisms, attempting to view the environment through their senses (Wiens 1989; Turner *et al.* 2001).

Herbivore ecology in a spatial-temporal context

Above, I have attempted to characterize the main themes covered in this thesis. The central, partly interrelated, issues throughout the entire thesis are the *scale*-dependency and *context*-dependency of species-environment relationships. As mentioned above, scale defines the spatial or temporal dimensions of an object or process, and determines the patterns that can be observed. I have discussed the relationships between species and their environment, and variation therein due to circadian fluctuations in environmental conditions (Chapter 2) and fluctuations over the seasons (Chapter 2 and 6). These patterns relate spatially to environmental variation over short distances (e.g., catenary gradients spanning some hundreds of meters), to spatial variation over large distances (e.g., broad gradients in altitude or resource distribution over many kilometres).

Context defines the circumstances in which an event occurs, i.e., the spatial and temporal setting within which species-environment relationships take place. I have discussed the influence of temporal context in terms of processes related to the period of the year and time of the day (Chapter 2), past use and memory (Chapter 3 and 4), and positive herbivore-vegetation feedbacks (Chapter 3). The influence spatial context is discussed in terms of the influence of the surroundings or neighbourhood of a site on the local, site-specific ecological phenomena (Chapter 2, 5 and 6).

I have tried to provide a wide array of examples to show the importance of explic-

itly considering the various aspects related to scale and context when studying species-environment relationships. These examples are illustrative, rather than comprehensive, and many more can be found in literature. They cover a wide range of systems (from the tropics to the arctic tundra, and from terrestrial to aquatic), and species (from small insects to mammalian megaherbivores), being indicative for the broad array of ecological investigations where the themes touched upon in this thesis are important. Collectively, these examples demonstrate the importance of considering issues of spatial-temporal scale and context in almost any ecological study.

Scale-dependency

Although it is easy to acknowledge that relationships between species and their environment are scale dependent (most ecologists now agree that scale is important when acquiring and interpreting ecological data), it is difficult to identify the right scales in practice (Turner *et al.* 2001; Wheatley & Johnson 2009). This is because scale issues occur in every facet of ecological research, from scales intrinsic to the ecological phenomenon under study, scales of observation and measurement, scales of analysis and modelling, and scales of management and policy (Bierkens *et al.* 2000; Wu *et al.* 2006). Because the scales intrinsic to ecological phenomena (e.g., a species' spatial scale of response to its environment) are often unknown, mismatches between the scales at which phenomena occur and the ones at which phenomena are studied might be more common than often acknowledged (Chapter 5; Holland *et al.* 2004; Wu *et al.* 2006).

When studying species-environment relationships, one deals with at least three components of scale: (1) the scales of environmental variation, (2) the scales at which species respond to this variation, and (3) the scales of data and analysis (Chapter 5). When studies on species-environment relationships are being used for management or policy, the scales at which management actions or policy take place are an additional scale component to the already three-layered system (Bierkens *et al.* 2000). This multiplicity of scale issues would not matter in a world where entities and relationships remain invariant across space or time, or in a landscape that is spatially or temporally homogenous (Wu 2007). However, as discussed above, landscapes are spatially and temporally heterogeneous, at various spatial and temporal scales, resulting in relationships between species and their environment that change across scales of analyses. Hence, the scales of observation and analyses have tremendous impact on the interpretation of what we think we know about systems and how they operate, which clearly has ramifications for most of the hotly contested areas in ecology (Mac Nally 2005).

Various studies showed that the quantification of environmental heterogeneity depends on the spatial scales of observation and analysis (Turner *et al.* 1989; Jelinski & Wu 1996; Wu *et al.* 2002; Fisher *et al.* 2004; Schmidt & Andrew 2005; A-Xing *et al.* 2008). Environmental heterogeneity may be expressed most strongly at specific spatial scales (Keitt *et al.* 1997; Keitt & Urban 2005; Murwira & Skidmore 2005; Dong *et al.* 2008), patterns that may dictate the scales at which organisms are forced to respond to environmental heterogeneity. For examples, environmental heterogeneity related to broad-scale altitudinal gradients (e.g., mountain ranges) or fine-scale topographic relief (e.g., catenary gradients) may dictate the scales at which, and ways in which, species respond to their environment (Chapter 2). This may even lead to contrasting species-environment relationships at different spatial scales. For example, in landscapes where altitude positively correlates with rainfall, but where local topography leads to run-off of

water from crest to valley-bottom, the abundance of species may be positively correlated to a broad-scale altitudinal gradient, yet negatively correlated to a fine-scale (local) altitudinal gradient (i.e., the catenary gradient), even though altitude at both spatial scales influences the species through the distribution of moisture, yet by means of different mechanisms.

This example can be used to highlight the importance of considering both grain and extent when quantifying landscape heterogeneity and when relating it to ecological responses, e.g., the distribution of a species in space. When the extent of a study is small relative to the scale of an important process, here for example the influence of a broad-scale altitudinal gradient on rainfall patterns and hence species abundance, the influence of this process on the phenomenon under study is likely not picked up by the analysis/analyst. Namely, the distance over which the process exerts influence on the phenomenon under study is large relative to the extent of the study, so that the large-scaled pattern may be considered to be homogeneous for the analysis, resulting in more fine-scaled patterns to dominate the analysis. Alternatively, if the gain size at which data are being analysed exceeds the distance over which fine-scaled processes take place (e.g., catenary run-off of water and nutrients), these processes are also likely to be missed by the analyst. What constitutes "broad" or "fine" here depends on the system and species under study.

Yet, since organisms respond to environmental characteristics at specific (but often unknown) scales, the spatial patterns resulting from a species' response to environmental patterns may differ from the spatial structure of the landscape (Chapter 5; Wagner & Fortin 2005). As discussed above and in chapter 5, analysing a species' response to its environment at a scale different from that at which the species responds to its environment has important ramifications for the estimation of the significance and strength of species-environment relationships. However, promising methods exist to study the scale-specific response of organisms to their environment, including moving window analyses (Chapter 5 and 6; Holland *et al.* 2004; Mayor *et al.* 2007), spatial filtering techniques using eigenvectors (Borcard & Legendre 2002; Borcard *et al.* 2004; Griffith & Peres-Neto 2006), and wavelet applications (Keitt & Urban 2005; Keitt & Fischer 2006).

The issues related to temporal scale resemble the issues regarding spatial scale. As discussed above and in chapter 2, environmental conditions may change temporarily over different time scales, e.g., in circadian or seasonal rhythms. Analyses of species-environment relationships have often not allowed such temporal variation, a serious limitation when confronted with real ecological systems. Organisms may occupy landscapes differently as the season progresses because of changes in the phenology of plants, changes in temperature, or changes in other factors to which organisms respond: under these circumstances, assessment of the relation between organisms and their environment would be misleading if time was influential but was left out of the analysis (Gutzwiller & Riffel 2007). Paralleling the influence of grain and extent in the spatial domain, analysing data with a temporal extent that is to short (e.g., a few days or weeks) leads to long-term patterns (e.g., seasonal or inter-annual) being not observed, while analysing data with a temporal resolution that is to coarse (e.g., one day) leads to short-term patterns (e.g., within-day) being unobserved.

Thus, variation in processes over different time scales can generate distinctive patterns that are overlooked or misunderstood when viewed from an inappropriate temporal resolution or extent (Boyce 2006). Hence, analysing patterns at different temporal

scales, varying both grain and extent, may lead to further insight into the processes that are at work to create the observed patterns. Although processes that vary over long time frames often generate patterns that vary spatially over large distances, this is not necessarily the case. For example, Chapter 2 shows that processes operating at different time scales (seasonal and circadian) generated spatial patterns in elephant distribution at the spatial scale of catenary gradients.

Our analytical approaches must thus incorporate temporal variation in explicit and robust ways (Gutzwiller & Riffel 2007). Methods to accommodate temporal variation in species-environment relationships include analyses at multiple temporal scales (Chapter 2; Fryxell *et al.* 2008), Fourier and wavelet analyses (Wittemyer *et al.* 2008), and state-space models or hidden Markov models (Patterson *et al.* 2008, 2009; Schick *et al.* 2008). Only when we can meaningfully extract ecological information from patterns in species-environment relationships across spatial and temporal scales, can we increase our understanding of the processes that are at work to create to observed spatial-temporal patterns in ecological phenomena.

Context-dependency

Context relates an event spatially to its neighbourhood or near surroundings, and temporarily to past conditions and events. As such, it is an integral part of most (ecological) phenomena, since these are generally not only depended on spatially and temporarily local attributes, but are influenced by landscape context and historical legacies (Levin 1992; Turner *et al.* 2001; Wiens & Donoghue 2004). Context is related to issues of spatial and temporal scale (i.e., extent and grain), since these constrain the range of possibilities at which context can be found to exert influence on phenomena (Chapter 5).

Beyond the ecological themes discussed here, spatial and temporal context are common and important aspects of everyday life. For example, context is a crucial part of the reading process (Pelli & Tillman 2007), as well as memory (Burgess *et al.* 2001a,b), thereby being fundamental to normal functioning in daily life. It has been argued that, in some circumstances, memory regarding events themselves and the spatial context within which events take place may dissociate (Burgess *et al.* 2001a). Moreover, spatial context is a key determinant of the value of real estate, so that "location, location, location" is the quintessential cliché in the real estate business (Atack & Margo 1998; Kiel & Zabel 2008). In cell biology, a similar adage can be applied to the regulation of cellular and organismal physiology: the location of a cell within an organism and the location within the cell of its constituent parts will affect all it does, including the functions it is capable of performing, its signaling partners, and whether and how it grows and divides (Hurtley 2009). At a totally different level, spatial context conditions the prospects for war and peace between states (Ward & Gleditsch 2002).

Returning to the realm of ecological investigations, ecologists and conservation biologists have begun to appreciate more fully the potential effects of the spatial and temporal context on the way organisms relate to their environment (Wiens 1989; Levin 1992; Turner *et al.* 2001; Gutzwiller & Riffel 2007). Hence, it is increasingly being acknowledged that spatial information should be used for more than simply overlaying data. The influence of spatial-temporal context on phenomena is therefore becoming to be an integral part of many ecological disciplines, e.g., (historical) biogeography (Wiens & Donoghue 2004) and community ecology (in the realms of both neutral and niche processes: Hubbell 2001; Kneitel & Chase 2004, respectively).

As discussed above and in Chapter 2, the spatial context regarding the abiotic landscape template influences the redistribution of resources and environmental conditions, thereby governing the spatial patterns in vegetation and hence the herbivores feeding upon it. Hence, I have highlighted the influence of considering local topographic position (e.g, crest or valley bottom) besides raw altitude (i.e., m a.s.l.) in studies on the biogeographical patterns of species abundances, since a given site (e.g., valley bottom) at 200 m a.s.l. might have a similar environment to another site at 650 m a.s.l., while at 200 m a.s.l. one can find a range of different local environments (e.g., valley, slope, crest) (Rennó *et al.* 2008). In other words, it is important to consider landscape context along with local site attributes when trying to explain local ecological processes (Turner *et al.* 2001).

Furthermore, the response of herbivores to and their influence on vegetation depends on spatial context, as herbivores often incorporate information regarding the quality of the landscape surrounding a site in their decisions concerning habitat selection (Chapter 3, 5 and 6; Senft *et al.* 1987; Bailey *et al.* 1996), and because foraging leads to a localised disturbance of the vegetation (Chapter 3). For example, Baraza *et al.* (2006) showed that neighbourhood matters for the conditional outcomes in plant-herbivore interactions, since herbivores avoided saplings that grew near to unpalatable shrubs. Moreover, elephants seldom roam far away from drinking water, so they may avoid areas with good forage characteristics that are to far from water, while they may also avoid water sources that are not associated with suitable vegetation (Harris *et al.* 2008; Van Aarde *et al.* 2008). It is thus necessary to introduce neighbourhood effects in analyses of plant-herbivore relationships.

Temporal context matters for the study of species-environment relationships, because patterns observed at midnight or during the dry season may differ drastically from those observed at midday or during the wet season, respectively (Chapter 2). Moreover, the presence of herbivores at a specific site may influence the future use of that site because it supplies them information regarding the habitat quality, and because it may initiate a positive feedback between herbivore and vegetation (Chapter 3 and 4). Furthermore, the temporal context constrains the possible locations within a landscape that can be reached by an individual within some amount of time. Together, this may lead to a high level of positive spatial-temporal autocorrelation over a short time frame, negative autocorrelation over intermediate time frames due to the depression of food resources when foraging, motivating foragers to move away from the resident site, and positive autocorrelation again over time frames long enough to allow the replenishment of food resources, making sites profitable to be revisited again (Chapter 4 and 5).

The importance of considering these issues *in toto*

So far, I have discussed the influence of various processes relating organisms to their abiotic and biotic environment, operating over a large variety of spatial and temporal scales. Together, this amalgam of interacting processes produces the spatial structure in the abundance of organisms, where different processes may create spatial patterns that may be observationally equivalent, and where spatial patterns in turn may influence a variety of processes (Turner *et al.* 2001; Wagner & Fortin 2005). The challenge for integrative ecology is thus to disentangle and quantify the relative importance of each of the above-mentioned components of species-environment relationships in determining the observed spatial patterns in species abundances (Wiens & Donoghue 2004; Legendre

et al. 2009). Hence, the sources of spatial structure in a species' distribution may be disentangled by distinguishing between organismally and physically generated environmental heterogeneity, and by distinguishing between spatial patterns due to exogenous predictors or due to endogenous processes. In all cases, when relating organisms to their environment, one has to explicitly consider issues of spatial scale, including the scales of spatial heterogeneity, the scales at which species resond to this heterogeneity, and the scales at which data are collected and analyses are conducted.

Given the complexity of most ecological systems and phenomena, it is understandable that many studies have simplified ecological systems by studying the effects of one component of species-environment relationships *per se,* in an attempt to make problems tractable. As necessary as this may be for methodological reasons, the spatial structure in ecological phenomena is derived from the synthesis of those individual imprints. Thus, a comprehensive model of species-environment relationships is unlikely to arise from studying individual component parts in isolation: it requires a synthesis of processes operating across a broad array of spatial en temporal scales. Having set out the component parts of species-environment relationships, what can be achieved by studying the individual components in concert? Is the saying that the whole is greater than the sum of its parts applicable to the study of species-environment relationships?

Casting the relationships between organisms and their environment in the context of hierarchy theory may sharpen our understanding of the influence of scale and context by emphasizing the linkages among different processes (Allen & Starr 1982; O'Neill *et al.* 1986; Senft *et al.* 1987; Wiens 1989; Turner *et al.* 2001). Hierarchy theory puts a collection of parts inside a whole through ordered relationships between different levels in the hierarchy, that is to say, upper levels are above lower levels, with relationships upward and downward. The levels within the hierarchy relate to entities from cells up to populations, and to processes that can be characterized by their rates of chance at different spatial and temporal scales. Large-scaled processes tend to have slow rates of change (e.g., the change of geomorphology, parent material, topography), whereas small-scaled processes change faster and more frequent (e.g., catenary water run-off, diet selection by herbivores) (Senft *et al.* 1987; Wu & Li 2006). Each level in the hierarchy is composed of subsystems of the next lower level, and is constrained by the level above it (Turner *et al.* 2001). A central issue in ecological investigations therefore concerns the respective roles of "top-down" (large-scaled processes determine the possibilities for small-scaled ones) and "bottom-up" (large-scaled patterns emerge from small-scaled processes) processes in determining the patterning in ecological phenomena (Mac Nally 2005). In reality, species-environment relationships are generally controlled by the simultaneous action of both top-down and bottom-up effects. Thus, these two types of relationships are not mutually exclusive, but should be viewed as complementary rather than opposing to each other (Wu *et al.* 2006).

Top-down effects

Large-scaled processes are often thought to have potentially large impacts on herbivores because they occur infrequently and constrain processes at lower levels (Senft *et al.* 1987; Bailey *et al.* 1996; Turner *et al.* 2001). For example, decisions regarding habitat selection at broad spatial and temporal scales (e.g., a seasonal migration to high altitude pastures or forests) constrain the options available for habitat and diet selection at finer spatial-temporal scales (e.g., the plant species available within these high altitude pastures or

forests) (Senft *et al.* 1987; Bailey *et al.* 1996). Similarly, selection of areas with a high availability or quality of forage at large spatial scales constrains the selection of small scale variation in forage characteristics, because a site may be situated within a matrix of attractive or repellent habitat (Chapter 3 and 5). Furthermore, elephants have to drink on average every two days (Van Aarde *et al.* 2008), so that the distance that they can travel within this time frame constrains the options available for habitat selection.

Abiotic processes operating at large scales may constrain or influence the way herbivores interact with their environment at small spatial-temporal scales. Namely, large-scale variation in climatic conditions can influence the effects of local topography on habitat selection by organisms, because animals may experience a catenary gradient differently at the wet site along a precipitation gradient versus a dry site along the gradient (Chapter 2). This applies to a precipitation gradient both in the temporal domain as well as in the spatial domain: a local catenary gradient may be experienced differently by organisms depending on the time of the year or location in space. A spatial rainfall gradient most likely yields patterns similar to the seasonal patterns found in Chapter 2. Moreover, the influence of the catenary gradient on the processes driving terrain-use by organisms depends on the way precipitation is distributed over time: rainfall occurring as discrete events, such as thunderstorms, typically are of short duration and high intensity, leading to run-off of water from crest to valleys (Venter *et al.* 2003). However, when rain is distributed more continuously over time and with a lesser intensity, the influence of catenary water run-off decreases. Thus, organisms interact with their environment within the context of coarse-scale, slower drivers determined by the physical template (Pickett *et al.* 2003).

Bottom-up effects

Although broad-scale processes may constrain and influence processes at smaller scales, the broad-scale patterns in species distributions may reflect the aggregate results of many small-scale foraging decisions (Senft *et al.* 1987; Romero *et al.* 2009). As mentioned above, the short-term responses of herbivores in terms of their movement in relation to resource density lead to varying population densities in space. Thus, local interaction can lead to large scale spatial patterns. This is increasingly being emphasized by theoretical ecologists, and the focus of much research on self-organization in natural systems. Self-organization is the process where large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions (Rietkerk *et al.* 2004; Rietkerk & Van de Koppel 2008). It is thus not imposed on a system from higher levels, but emerges from fine-scale interactions owing to internal causes (Rietkerk *et al.* 2004). As an example, in Chapter 3 I showed that large-scale vegetation patterning only occurs when considering the interacting effects of (1) spatially explicit foraging by herbivores and (2) positive plant-herbivore feedbacks. Considering these effects in isolation did not result in large-scale vegetation patterning, and the vegetation patterns only emerged when these processes could interact (see Fig. 3.3). The model of Chapter 3 thus shows the effects of localized positive feedback processes that act within the context of a global constraint. In somewhat modified form, the model presented in this Chapter 3 resembles the class of self-organizing processes known as localized disturbance-recovery processes, where disturbances occur primarily close to a site already disturbed (e.g., by wind or herbivory) and recovery takes place primarily close to a site that is occupied by organisms (e.g., by local seed dispersal) (Rietkerk & Van de Koppel 2008).

Along the lines of thought presented in Chapter 2 and 3, I hypothesize that catenary topography influences the broad-scale distribution patterns of savanna herbivores, through the interacting effects of the processes of water and nutrient redistribution along the catenary gradient with positive plant-herbivore interactions. The catenary redistribution of water and soil nutrients enhances the (re)growth of vegetation at water run-on areas (Chapter 2), even to the extent that broad-scale vegetation productivity may be higher than could be expected solely from rainfall alone (Noy-Meir 1973; Tongway & Ludwig 2005; Buis *et al.* 2009). This is the reverse of the classic logic in higher rainfall climatic zones and is a cornerstone of the ecology of arid lands (Tongway & Ludwig 2005). The reasoning behind this goes back to the large number of small rainfall events and the small number of large ones referred to above, and is invoked by the concept of a critical threshold in the availability of a scarce resource, in this case water (Sankaran *et al.* 2005; Tongway & Ludwig 2005). The concentration of water and nutrients at specific water run-on sites (e.g., valley bottoms) creates hotspots of abundant and fertile vegetation (Nellemann *et al.* 2002; Grant & Scholes 2006), what might attract grazing and browsing herbivores in otherwise nutrient-poor savannas. Thus, the small scale process of resource redistribution may lead to an increase in the broad-scale density of herbivores.

Since large herbivores may increase the level of soil differentiation along a catenary gradient through increasing the erosion of soil particles, they may enhance this positive effect of land surface undulations on the productivity of vegetation (Hartshorn *et al.* 2009). Moreover, the herbivores may exhibit a positive browse-browser feedback loop, especially at the lower parts of the catena. Due to the increased soil fertility there, and the positive effects of herbivory on plant productivity (Chapter 3; Nunez-Farfan *et al.* 2007; Kohi *et al.* 2010), the herbivores may even increase the productivity of the vegetation at the lower parts of the catena on top of their influence on soil differentiation. Thus, the lower parts of a catena may be disproportionately important to the foraging process of herbivores, and hence to their broad scale distribution patterns. This may be the reason why Asner *et al.* (2009) recently found the vegetation at the lower parts of the catena to be more heavily impacted by herbivores than the vegetation in the upland part of the catena. Moreover, several studies showed that trees can improve the overall quality of savanna grasses by enhancing grass growth and nutrient uptake during the wet season, delaying grass wilting in the dry season, elevating soil nutrient concentrations beneath their crowns, reducing the intensity of solar radiation, and reducing evapotranspiration and soil temperature (e.g., Belsky 1989; Ludwig *et al.* 2003; Treydte *et al.* 2007; Ludwig *et al.* 2008; Treydte *et al.* 2008). Hence, not only browsers may show responses to landscape undulations but similar patterns are to be expected for grazers.

Conclusion and outlook

Understanding species-environment relationships requires recognition of the complexity of factors responsible for creating spatial patterning in a species' abundance, including the influence of physically created environmental heterogeneity, the role of organisms in creating heterogeneity, plant-herbivore feedbacks, and the influence of endogenous processes (e.g., memory, dispersal limitation) on a species' spatial distribution pattern. Furthermore, understanding species-environment relationships requires an explicit focus on issues of spatial and temporal scale, distinguishing between scales intrinsic to environmental heterogeneity, scales intrinsic to a species' response to this heterogeneity, and the scales at which data is collected and analyses conducted. The challenge is thus to

observe and analyze species-environment relationships at scales relevant to the patterns and processes being studied.

Instead of studying the separate components of species-environment relationships in isolation, a unitary treatment opens exciting avenues for the analysis and understanding of spatial variation in ecological phenomena. Namely, the interactions between spatially and temporally changing organismal behaviour on the one hand, and environmental heterogeneity on the other hand, may lead to broad scale patterns in ecological phenomena that differ from predictions based on the small scale (local) processes. An integral approach that couples organisms to their environment is thus needed, an approach that recognizes the fact that processes act on a range of spatial and temporal scales, and are affected by spatial-temporal context. Such processes range from detailed movement responses to the resources encountered *en route*, to the processes responsible for creating a spatially and temporally heterogeneous abiotic template that forms the basis of the landscape where organisms live in.

Thus, it must be recognized that the movement of organisms, but especially that of sentient animals, is a complex process that depends on both an organism's ability to perform various tasks and the nature of the landscape through which it moves (Getz & Saltz 2008; Nathan 2008). These tasks include the organism's intrinsic ability to move, the organism's internal state to perform certain activities (e.g., forage, seek shelter, head home, flee, or seek a mate), and the organism's ability to sense its environment, remember landmarks, construct mental maps, and process information (Getz & Saltz 2008; Nathan 2008). Landscape variables that influence organismal movement include topography, abiotic conditions (e.g., temperature and wind speed), and the distribution and abundance of resources (e.g., forage and water) (Bailey & Provenza 2008; Nathan 2008; Gurarie *et al.* 2009). Because the behaviour of organisms and the landscape they move through change over time, the dynamics of species-environment relationships should be considered.

In this thesis, I have shown that organisms respond to environmental heterogeneity at species-specific (Chapter 5 and 6) and process-specific (Chapter 2) scales. These scales may differ from the scales of observation, analysis or prediction, leading to scale effects that may have profound influences on conclusions and predictions. Namely, analyses at fine scales may miss important patterns and processes operating on broader scales, while broad-scale observations may not have enough detail necessary to understand fine-scale dynamics. Besides issues of scale, I have shown that the issue of spatial and temporal context is important for the study of species-environment relationships. Namely, it influences the feedbacks between herbivores and vegetation (Chapter 3), the processes leading to spatial heterogeneity regarding resources and environmental conditions, thereby influencing the patterns of space usage by organisms (Chapter 2), the influence of past use in determining organismal movement (Chapter 3 and 4), the influence of the neighbouring landscape on habitat selection by organisms (Chapter 3, 5 and 6).

Understanding the different components of the spatial-temporal context within which species interact with their environment is thus crucial, and the challenge is to disentangle and quantify the relative importance of each component (Wiens & Donoghue 2004; Legendre *et al.* 2009). Spatially explicit, organism-centered studies focusing on the spatial-temporal context of species-environment relationships may ultimately lead to a more accurate understanding and prediction of species distributions (Chapter 5 and 6). The challenges involved in making better predictions of species' distributions are

both applied and theoretical (Guisan *et al.* 2006). For example, scientists and managers need reliable predictions of species' distributions to evaluate properly the impact of climate and land-use changes on the distribution, composition, structure and functioning of communities and ecosystems (Guisan *et al.* 2006; Holyoak *et al.* 2008). This is eminently useful for ecosystem management and landscape planning; for invasive species biology (e.g., Holyoak *et al.* 2008); for understanding and managing the spread and abundance of infectious diseases (e.g., Ostfeld *et al.* 2005); for the economics of natural resources (e.g., Bulte *et al.* 2004); and for understanding landscape genetics and gene flow (e.g., Wang *et al.* 2008).

Advancement in the technologies and tools for analyses available to researchers and ecosystem managers offers a plethora of possibilities to advance our understanding of species-environment relationships. However, a critical requisite is that they are being studied with an explicit awareness of scaling issues and the importance of the spatial-temporal context. I have demonstrated methods to explicitly consider such issues when studying species-environment relationships, and have discussed these for a wide variety of ecosystems and taxa. The issues of scale and context should be considered from both a landscape perspective, as well as a species-specific perspective, and the scales of data collection and analyses are critical therein. Through explicitly considering the issues of spatial-temporal scale and context when studying species-environment relationships, ecologists can advance the understanding of the core theme of ecology as a scientific discipline, namely the interactions that determine the distribution and abundance of organisms.

Bibliography

A-Xing ZHU, Burt JE, Smith M, Rongxun W & Jing GAO (2008). The impact of neighbourhood size on terrain derivatives and digital soil mapping. *In* Q Zhou, B Lees & G Tang, eds., *Advances in Digital Terrain Analysis*, 333–348. Springer, Berlin.

Addicott JF, Aho JM, Antolin MF, Richardson JS & Soluk DA (1987). Ecological neighbourhoods: scaling environmental patterns. *Oikos* 49: 340–346.

Adler P, Raff D & Lauenroth WK (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479.

Ager AA, Johnson BK, Kern JW & Kie JG (2003). Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy* 84: 1076–1088.

Agrawal AA (1998). Induced responses to herbivory and increased plant performance. *Science* 279: 1201–1202.

Allen T & Starr T (1982). *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago.

Anderson TM, Ritchie ME, Mayemba E, Eby S, Grace JB & McNaughton SJ (2007). Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. *American Naturalist* 170: 343–357.

Anselin L (2002). Under the hood - Issues in the specification and interpretation of spatial regression models. *Agricultural Economics* 27: 247–267.

Anselin L (2006). How (not) to lie with spatial statistics. *American Journal of Preventive Medicine* 30: S3–S6.

Anselin L (2009). Spatial regression. *In* AS Fotheringham & PA Rogerson, eds., *The SAGE handbook of spatial analysis*, 255–275. SAGE Publications Ltd, Los Angeles.

Anselin L, Florax RJGM & Rey SJ (2004). *Advances in spatial econometrics - methodology, tools and applications*. Springer Verlag, Berlin.

Araújo MB & Guisan A (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33: 1677–1688.

Archer SR (1990). Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. *Journal of Biogeography* 17: 453–462.

Archer SR, Scrifres C, Bassham CR & Maggio R (1988). Autogenic succession in a subtropical savanna: conversion of grassland to Thorn woodland. *Ecological Monographs* 58: 111–127.

Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS & Martin RE (2009). Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences* 106: 4947–4952.

Atack J & Margo RA (1998). "Location, Location, Location!" The price gradient for vacant urban land: New York, 1835 to 1900. *The Journal of Real Estate Finance and Economics* 16: 151–172.

Augustine DJ & McNaughton SJ (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41: 45–58.

Austin MP (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157: 101–118.

Ayinde K (2007). A comparative study of the performances of the OLS and some GLS estimators when stochastic regressors are both collinear and correlated with error terms. *Journal of Mathematics and Statistics* 3: 196–200.

Babb SJ & Crystal JD (2006). Episodic-like memory in the rat. *Current Biology* 16: 1317–1321.

Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM & Sims PL (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386–400.

Bailey DW & Provenza FD (2008). Mechanisms determining large-herbivore distribution. *In* HHT Prins & F Van Langevelde, eds., *Resource ecology - Spatial and temporal dynamics of foraging*, 7–28. Springer, Dordrecht.

Bakker JP, Leeuw J & Wieren SE (1984). Micro-patterns in grassland vegetation created and sustained by sheep-grazing. *Plant Ecology* 55: 153–161.

Baraza E, Zamora R & Hodar A (2006). Conditional outcomes in plant-herbivore interactions: neighbours matter. *Oikos* 113: 148–156.

Barnes RFW (1983). The elephant problem in Ruaha National Park, Tanzania. *Biological Conservation* 26: 127–148.

Barraquand F & Benhamou S (2008). Animal movements in heterogeneous landscapes: identifying profitable places and homogenous movement bouts. *Ecology* 89: 3336–3348.

Bartumeus F (2009). Behavioral intermittence, Lévy patterns, and randomness in animal movement. *Oikos* 118: 488–494.

Bartumeus F, Da Luz MGE, Viswanathan GM & Catalan J (2005). Animal search strategies: a quantative random-walk analysis. *Ecology* 86: 3078–3087.

Bartumeus F, Peters F, Pueyo S, Marrase C & Catalan J (2003). Helical levy walks: adjusting searching statistics to resource availability in microzooplankton. *Proceedings of the National Academy of Sciences* 100: 12771–12775.

Basille M, Calenge C, Marboutin E, Andersen R & Gaillard JM (2008). Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. *Ecological Modelling* 211: 233–240.

Beale CM, Lennon JJ, Elston DA, Brewer MJ & Yearsley JM (2007). Red herrings remain in geographical ecology: a reply to Hawkins et al. (2007). *Ecography* 30: 845–847.

Beauchamp G & Ruxton GD (2005). Harvesting resources in groups or alone: the case of renewing patches. *Behavioral Ecology* 16: 989–993.

Begon M, Harper JL & Townsend CR (1996). *Ecology: individuals, populations and communities. Third edition*. Blackwell Science, Oxford.

Bell RHV (1971). A grazing ecosystem in the Serengeti. *Scientific American* 224: 86–93.

Bell WJ (1991). *Searching behaviour - the behavioural ecology of finding resources*. Chapman and Hall, London.

Belsky AJ (1989). The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* 26: 1005–1024.

Ben Shahar R (1990). Soil nutrients distribution and moisture dynamics on upper catena in a semi-arid nature reserve. *Plant Ecology* 89: 69–77.

Ben Shahar R (1993). Patterns of elephant damage to vegetation in Northern Botswana. *Biological Conservation* 65: 249–256.

Ben Shahar R & Macdonald DW (2002). The role of soil factors and leaf protein in the utilization of mopane plants by elephants in northern Botswana. *BMC Ecology* 2: 1–6.

Benhamou S & Bovet P (1989). How animals use their environment: a new look at kinesis. *Animal Behaviour* 38: 375–383.

Bergman CM, Schaefer JA & Luttich SN (2000). Caribou movement as a correlated random walk. *Oecologia* 123: 364–374.

Betts MG, Ganio LM, Huso MMP, Som NA, Huettman F, Bowman J & Wintle BA (2009). The ecological importance of space in species distribution models: a comment on Dormann et al. *Ecography* 32: 374–378.

Bierkens MFP, Finke PA & De Willigen P (2000). *Upscaling and downscaling methods for environmental research*. Kluwer, Dordrecht.

Bini LM, Diniz-Filho JAF, Rangel TFLVB, Akre TSB, Albaladejo RG, Albuquerque FS, Aparicio A, Araújo MB, Baselga A, Beck J *et al.* (2009). Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography* 32: 193–204.

Bivand R (2009). spdep: spatial dependence: weighting schemes, statistics and models. R package version 0.4-34.

Bjornstad ON (2009). ncf: spatial nonparametric covariance functions. R package version 1.1-2.

Boisvert MJ & Sherry DF (2006). Interval timing by an invertebrate, the bumble bee Bombus impatiens. *Current Biology* 16: 1636–1640.

Bond WJ, Midgley GF & Woodward FI (2003). The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* 9: 973–982.

Borcard D & Legendre P (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153: 51–68.

Borcard D, Legendre P, Avois-Jacquet C & Tuomisto H (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85: 1826–1832.

Borcard D, Legendre P & Draqeau P (1992). Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.

Boscolo D & Metzger J (2009). Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? *Landscape Ecology* 24: 907–918.

Boyce MS (2006). Scale for resource selection functions. *Diversity and Distributions* 12: 269–276.

Boyce MS, Vernier PR, Nielsen SE & Schmiegelow FKA (2002). Evaluating resource selection functions. *Ecological Modelling* 157: 281–300.

Bradburn MJ, Clark TG, Love SB & Altman DG (2003a). Survival analysis part II: multivariate data analysis - an introduction to concepts and methods. *British Journal of Cancer* 89: 431–436.

Bradburn MJ, Clark TG, Love SB & Altman DG (2003b). Survival analysis part III: multivariate data analysis - choosing a model and assessing its adequacy and fit. *British Journal of Cancer* 89: 605–611.

Brady M, McAlpine C, Miller C, Possingham H & Baxter G (2009). Habitat attributes of landscape mosaics along a gradient of matrix development intensity: matrix management matters. *Landscape Ecology* 24: 879–891.

Brennan J, Bender D, Contreras T & Fahrig L (2002). Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. *In* J Liu & WW Taylor, eds., *Integrating landscape ecology into natural resource management*, 67–91. Cambridge University Press.

Breshears DD (2006). The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* 4: 96–104.

Börger L, Dalziel BD & Fryxell JM (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters* 11: 637–650.

Brown JS (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22: 37–47.

Bucini G, Hanan NP, Boone RB, Smit IPJ, Saatchi S, Lefsky MA & Asner GP (2010). Woody fractional cover in Kruger National Park, South Africa: remote-sensing-based maps and ecological insights. *In Ecosystem function in savannas: measurement and modeling at landscape to global scales*, –. CRC/Taylor and Francis.

Buis G, Blair J, Burkepile D, Burns C, Chamberlain A, Chapman P, Collins S, Fynn R, Govender N, Kirkman K *et al.* (2009). Controls of aboveground net primary production in mesic savanna grasslands: an inter-hemispheric comparison. *Ecosystems* 12: 982–995.

Bulte E, Damania R, Gillson L & Lindsay WK (2004). Space - The final frontier for economists and elephants. *Science* 306: 420–421.

Burgess N, Becker S, King JA & O'Keefe J (2001a). Memory for events and their spatial context: models and experiments. *Philosophical Transactions of the Royal Society of London B* 356: 1493–1503.

Burgess N, Maguire EA, Spiers HJ & Keefe J (2001b). A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *NeuroImage* 14: 439–453.

Calenge C (2006). The package "Adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519.

Calenge C & Basille M (2008). A general framework for the statistical exploration of the ecological niche. *Journal of Theoretical Biology* 252: 674–685.

Calenge C, Darmon G, Basille M, Loison A & Jullien JM (2008). The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology* 89: 555–566.

Calenge C, Maillard D, Gaillard JM, Merlot L & Peltier R (2002). Elephant damage to trees of wooded savanna in Zakouma National Park, Chad. *Journal of Tropical Ecology* 18: 599–614.

Cartar RV (2004). Resource tracking by bumble bees: responses to plant-level differences in quality. *Ecology* 85: 2764–2771.

Caylor KK, Dowty PR, Shugart HH & Ringrose S (2004). Relationship between small-scale structural variability and simulated vegetation productivity across a regional moisture gradient in southern Africa. *Global Change Biology* 10: 374–382.

Caylor KK & Shugart HH (2006). Pattern and process in savanna ecosystems. *In* P D'Odorico & A Porporato, eds., *Dryland Ecohydrology*, 259–281. Springer, Dordrecht.

Chamaille-Jammes S, Valeix M & Fritz H (2007a). Elephant management: why can't we throw out the babies with the artificial bathwater? *Diversity and Distributions* 13: 663–665.

Chamaille-Jammes S, Valeix M & Fritz H (2007b). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-

water availability. *Journal of Applied Ecology* 44: 625–633.

Chamran F, Gessler PE & Chadwick OA (2002). Spatially explicit treatment of soil-water dynamics along a semiarid catena. *Soil Science Society of America Journal* 66: 1571–1583.

Charnov EL (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136.

Cid MS & Brizuela MA (1998). Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *Journal of Range Management* 51: 644–649.

Clark TG, Bradburn MJ, Love SB & Altman DG (2003). Survival analysis part I: basic concepts and first analyses. *British Journal of Cancer* 89: 232–238.

Clayton NS & Dickinson A (1998). Episodic-like memory during cache recovery by scrub jays. *Nature* 395: 272–274.

Cliff A & Ord J (1981). *Spatial processes: models and applications*. Pion, London.

Clifford P, Richardson S & Hemon D (1989). Assessing the significance of the correlation between two spatial processes. *Biometrics* 45: 123–134.

Collett M (2009). Spatial memories in insects. *Current Biology* 19: R1103–R1108.

Colman JE, Mysterud A, Joprgensen NH & Moe SR (2009). Active land use improves reindeer pastures: evidence from a patch choice experiment. *Journal of Zoology* 279: 358–363.

Coppock DL, Detling JK, Ellis JE & Dyer MI (1983). Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plants species diversity. *Oecologia* 56: 1–9.

Coughenour MB (1991). Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44: 530–542.

Couteron P & Kokou K (1997). Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology* 132: 211–227.

Cox DR (1972). Regression models and life-tables. *Journal of the Royal Statistical Society. Series B (Methodological)* 34: 187–220.

Cressie NAC (1991). *Statistics for spatial data*. John Wiley and sons, New York.

Crist TO, Guertin DS, Wiens JA & Milne BT (1992). Animal movement in heterogeneous landscapes: an experiment with Eleodes beetles in shortgrass prairie. *Functional Ecology* 6: 536–544.

Crystal JD (2006). Animal behavior: timing in the wild. *Current Biology* 16: R252–R253.

Currie DJ (2007). Disentangling the roles of environment and space in ecology. *Journal of Biogeography* 34: 2009–2011.

Cushman SA, Chase M & Griffin C (2005). Elephants in space and time. *Oikos* 109: 331–341.

Cushman SA & McGarigal K (2002). Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology* 17: 637–646.

Cushman SA & McGarigal K (2004). Patterns in the species-environment relationship depend on both scale and choice of response variables. *Oikos* 105: 117–124.

Davis JM & Stamps JA (2004). The effect of natal experience on habitat preferences. *Trends in Ecology an Evolution* 19: 411–416.

De Knegt HJ, Groen TA, Van de Vijver CADM, Prins HHT & Van Langevelde F (2008). Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos* 117: 543–554.

De Knegt HJ, Hengeveld GM, Van Langevelde F, De Boer WF & Kirkman KP (2007). Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology* 18: 1065–1072.

De Knegt HJ, Van Langevelde F, Coughenour MB, Skidmore AK, De Boer WF, Heitkönig IMA, Knox N, Slotow R, Van der Waal C & Prins HHT (2010). Spatial autocorrelation and the scaling of species-environment relationships. *Ecology* In press.

De Ridder N & van Keulen H (1995). Estimating biomass through transfer functions based on simulation model results: a case study for the Sahel. *Agricultural Water Management* 28: 57–71.

Del Mar Delgado M & Penteriani V (2008). Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *The American Naturalist* 172: 475–485.

Diez J & Pulliam H (2007). Hierarchical analysis of species distributions and abundance across environmental gradients. *Ecology* 88: 3144–3152.

Diniz-Filho JAF & Bini LM (2005). Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography* 14: 177–185.

Diniz-Filho JAF, Bini LM & Hawkins BA (2003). Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* 12: 53–64.

Diniz-Filho JAF, Hawkins A, Bini LM, De Marco P & Blackburn M (2007). Are spatial regression methods a panacea or a Pandora's box? A reply to Beale et al. (2007). *Ecography* 30: 848–851.

Dong X, Nyren P, Patton B, Nyren A, Richardson J & Maresca T (2008). Wavelets for agriculture and biology: a tutorial with applications and outlook. *BioScience* 58: 445–453.

Dormann CF (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography* 16: 129–138.

Dormann CF (2009). Response to Comment on 'Methods to account for spatial autocorrelation in the analysis of species distributional data: a review'. *Ecography* 32: 379–381.

Dormann CF, McPherson M, Araújo B, Bivand R, Bolliger J, Carl G, Davies G, Hirzel A, Jetz W, Kissling WD *et al.* (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628.

Dormann CF & Seppelt R (2007). Do organisms use landscape at certain spatial scales? A null model for diversity pattern in relation to the spatial extend of landscapes. *In* B Shchröder, H Reuter & B Reineking, eds., *Multiple scales in ecology*, 35–42. Peter Lang, Internationaler Verlag de Wissenschaften, Frankfurt am Main.

Drapela T, Moser D, Zaller G & Frank T (2008). Spider assemblages in winter oilseed rape affected by landscape and site factors. *Ecography* 31: 254–262.

Drescher M, Heitkönig IMA, Van den Brink PJ & Prins HHT (2006). Effects of sward structure on herbivore foraging behaviour in a South African savanna: An investigation of the forage maturation hypothesis. *Austral Ecology* 31: 76–87.

Du Toit JT (2003). Large herbivores and savanna heterogeneity. *In* JT Du Toit, HC Biggs & K Rogers, eds., *The Kruger experience: ecology and management of savanna heterogeneity*, 292–309. Island Press, Washington, DC.

Du Toit JT, Biggs HC & Rogers K (2003). *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, DC.

Du Toit JT, Bryant JP & Frisby K (1990). Regrowth and palatability of acacia shoots following pruning by african savanna browsers. *Ecology* 71: 149–154.

Dungan JL, Perry JN, Dale MRT, Legendre P, Citron-Pousty S, Fortin MJ, Jakomulska A, Miriti M & Rosenberg MS (2002). A balanced view of scale in spatial statistical analysis. *Ecography* 25: 626–640.

Dutilleul P, Clifford P, Richardson S & Hemon D (1993). Modifying the t test for assessing the correlation between two spatial processes. *Biometrics* 49: 305–314.

Eacott MJ, Easton A & Zinkivskay A (2005). Recollection in an episodic-like memory task in the rat. *Learning and Memory* 12: 221–223.

Eagleson PS & Segarra RI (1985). Water limited equilibrium of savanna vegetation systems. *Water Resources Research* 21: 1483–1493.

Ebbes P, Wedel M, Böckenholt U & Steerneman T (2005). Solving and testing for regressor-error (in)dependence when no instrumental variables are available: with new evidence for the effect of education on income. *Quantitative Marketing and Economics* 3: 365–392.

Elith J & Leathwick JR (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.

Engler R, Guisan A & Rechsteiner L (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41: 263–274.

Erwin DH (2008). Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology and Evolution* 23: 304–310.

Etherington TR, Ward AI, Smith GC, Pietravalle S & Wilson GJ (2009). Using the Mahalanobis distance statistic with unplanned presence-only survey data for biogeographical models of species distribution and abundance: a case study of badger setts. *Journal of Biogeography* 36: 845–853.

Fernandez-Illescas CP & Rodriguez-Iturbe I (2003). Hydrologically driven hierarchical competition-colonization models: the impact of interannual climate fluctuations. *Ecological Monographs* 73: 207–222.

Fisher P, Wood J & Cheng T (2004). Where is Helvellyn? Fuzziness of multi-scale landscape morphometry. *Transactions of the Institute of British Geographers* 29: 106–128.

Florax R & Folmer H (1992). Specification and estimation of spatial linear regression models: Monte Carlo evaluation of pre-test estimators. *Regional Science and Urban Economics* 22: 405–432.

Fornara DA & Toit JTD (2007). Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88: 200–209.

Fortin MJ & Dale MRT (2005). *Spatial analysis: a guide for ecologists*. Cambridge University Press.

Fortin MJ & Melles SJ (2009). Avian spatial responses to forest spatial heterogeneity at the landscape level: conceptual and statistical challenges. *In* S Miao, S Carstenn & M Nungesser, eds., *Real world ecology - large-scale and long-term case studies and methods*, 137–160. Springer, New York.

Frair JL, Merrill EH, Visscher DR, Fortin D, Beyer HL & Morales JM (2005). Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20: 273–287.

Fretwell SD & Lucas HL (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16–36.

Fryxell JM, Hazell M, Börger L, Dalziel BD, Haydon DT, Morales JM, McIntosh T & Rosatte

RC (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences* 105: 19114–19119.

Fryxell JM & Sinclair ARE (1988). Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution* 3: 237–241.

Gambiza J, Bond W, Frost PGH & Higgins S (2000). Land use options in dry tropocal woodland ecosystems in Zimbabwe: a simulation model of miombo woodland dynamics under different management regimes. *Ecological Economics* 33: 353–368.

Gautestad AO & Mysterud I (2005). Intrinsic scaling complexity in animal dispersion and abundance. *American Naturalist* 165: 44–55.

Getz WM & Saltz D (2008). A framework for generating and analyzing movement paths on ecological landscapes. *Proceedings of the National Academy of Sciences* 105: 19066–19071.

Gibson RN, Pihl L, Burrows MT, Modin J, Wennhage H & Nickell LA (1998). Diel movements of juvenile plaice Pleuronectes platessa in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* 165: 145–159.

Gill FB (1988). Trapline foraging by Hermit Hummingbirds: competition for an undefended, renewable resource. *Ecology* 69: 1933–1942.

Goodwin BJ & Fahrig L (2002). Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*. *Canadian Journal of Zoology* 80: 24–35.

Gordon IJ & Lindsay WK (1990). Could mammalian herbivores manage their resources? *Oikos* 59: 270–280.

Gotway CA & Young LJ (2002). Combining incompatible spatial data. *Journal of the American Statistical Association* 97: 632–648.

Graham MH (2003). Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.

Grainger M, Van Aarde R & Whyte I (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology* 43: 369–375.

Grambsch PM & Therneau TM (1994). Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81: 515–526.

Grant CC, Bengis R, Balfour D & Peel M (2008). Controlling the distribution of elephants. *In* RJ Scholes & K Mennell, eds., *Elephant management: a scientific assessment of South Africa*, 329–369. Witwatersrand University Press, Johannesburg, South Africa.

Grant CC & Scholes MC (2006). The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation* 130: 426–437.

Greenwood PJ & Harvey PH (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1–21.

Greig-Smith P (1979). Pattern in vegetation. *Journal of Ecology* 67: 755–779.

Greyling MD (2004). *Sex and age related distinctions in the feeding ecology of the Afrcan elephant, Loxodonta africana*. Ph.D. thesis, University of the Witwatersrand, Johannesburg.

Griffith DA & Peres-Neto PR (2006). Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87: 2603–2613.

Guisan A, Graham C, Elith J & Huettmann F (2007). Sensitivity of predictive species

distribution models to change in grain size. *Diversity and Distributions* 13: 332–340.

Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMC, Aspinall R & Hastie T (2006). Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology* 43: 386–392.

Guisan A & Thuiller W (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009.

Gurarie E, Andrews RD & Laidre KL (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters* 12: 395–408.

Gutzwiller K & Riffel S (2007). Using statistical models to study temporal dynamics of animal-landscape relations. *In* JA Bissonette & I Storch, eds., *Temporal dimensions of landscape ecology - wildlife responses to variable resources*, 93–118. Springer, New York.

Haining RP (2003). *Spatial data analysis: theory and practice*. Cambridge University Press, Cambridge, UK.

Hakeem AY, Hof PR, Sherwood CC, Switzer RC, Rasmussen LEL & Allman JM (2005). Brain of the African elephant (*Loxodonta africana*): Neuroanatomy from magnetic resonance images. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology* 287A: 1117–1127.

Harris GM, Russell GJ, Van Aarde RI & Pimm SL (2008). Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* 42: 66–75.

Hartshorn AS, Khomo L, Dixon J, C B, Kurtz A, Heimsath A, Rogers K & Chadwick OA (2009). The tempo of soil differentiation along granitic catenas: How poor soils get poorer and rich soils get richer. *In The 94th ESA Annual Meeting*. Albuquerque, New Mexico.

Hawkins BA, Diniz-Filho JA, Bini LM, De Marco P & Blackburn TM (2007). Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. *Ecography* 30: 375–384.

Henderson J, Hurly TA, Bateson M & Healy SD (2006). Timing in free-living rufous hummingbirds, *Selasphorus rufus*. *Current Biology* 16: 512–515.

Hengeveld G, van Langevelde F, Groen TA & De Knegt H (2009). Optimal foraging for multiple resources in several food species. *The American Naturalist* 174: 102–110.

Higgins SI, Bond WJ & Trollope WSW (2000). Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213–229.

Hijmans RJ, Cameron S & Parra J (2007). WorldClim, Version 1.4. University of California, Berkeley. http://www.worldclim.org.

HilleRisLambers R, Rietkerk M, Van den Bosch F, Prins HHT & De Kroon H (2001). Vegetation pattern formation in semi-arid grazing systems. *Ecology* 82: 50–61.

Hirzel AH & Arlettaz R (2003). Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environmental Management* 32: 614–623.

Hirzel AH, Hausser J, Chessel D & Perrin N (2002). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83: 2027–2036.

Hirzel AH & Le Lay G (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45: 1372–1381.

Hirzel AH, Le Lay G, Helfer V, Randin C & Guisan A (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199: 142–152.

Hirzel AH, Posse B, Oggier PA, Crettenand Y, Glenz C & Arlettaz R (2004). Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *Journal of Applied Ecology* 41: 1103–1116.

Hobbs NT (1996). Modification of ecosystems by ungulates. *The Journal of Wildlife Management* 60: 695–713.

Hobbs NT (1999). Responses of large herbivores to spatial heterogeneity in ecosystems. *In* H Jung & G Fahey, eds., *Nutritional ecology of herbivores: proceedings of the Vth international symposium of the nutrition of herbivores*, 97–129. American Society of Animal Science, Savoy, Illinois, USA.

Holland JD, Bert DG & Fahrig L (2004). Determining the spatial scale of species' response to habitat. *BioScience* 54: 227–233.

Holyoak M, Casagrandi R, Nathan R, Revilla E & Spiegel O (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* 105: 19114–19119.

House JI, Archer S, Breshears DD & Scholes RJ (2003). Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography* 30: 1763–1777.

Hubbell SP (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey.

Huisman J, Grover JP, Van der Wal R & Van Andel J (1997). Competition for light, plant-species replacement and herbivore abundance along productivity gradients. *In* H Olff, VK Brown & RH Drent, eds., *Herbivores: between plants and predators*, 239–269. Blackwell Science, Oxford.

Huntley BJ & Walker BH (1982). *Ecology of tropical savannas*. Springer, Berlin.

Hurtley S (2009). Location, Location, Location. *Science* 326: 1205–1205.

Ibánez I, Silander JA, Wilson AM, LaFleur N, Tanaka N & Tsuyama I (2009). Multivariate forecasts of potential distributions of invasive plant species. *Ecological Applications* 19: 359–375.

Jachmann H & Bell RHV (1985). Utilization by elephants of the Brachystegia woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* 23: 245–258.

Janssen P, Fortin D & Hébert C (2009). Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. *Ecography* 32: 423–432.

Jarvis A, Reuter H, Nelson A & Guevara E (2008). Hole-filled seamless SRTM data V4, Consortium for Spatial Information, International Centre for Tropical Agriculture, http://srtm.csi.cgiar.org.

Jefferies RL, Klein DR & Shaver GR (1994). Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos* 71: 193–206.

Jelinski D & Wu J (1996). The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology* 11: 129–140.

Jeltsch F, Milton SJ, Dean WRJ, Rooyen N & Moloney KA (1998). Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* 86: 780–793.

Jeltsch F, Milton SJ, Dean WRJ & Van Rooyen N (1996). Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* 84: 583–595.

Jeltsch F, Weber GE & Grimm V (2000). Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* 150: 161–171.

Johnson CJ, Nielsen SE, Merrill EH, McDonald TL & Boyce MS (2006). Resource selection functions based on use-availability data: theoretical motivation and evaluation

methods. *Journal of Wildlife Management* 70: 347–357.

Johnson CJ, Seip DR & Boyce MS (2004). A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41: 238–251.

Jones CG, Lawton JH & Shachak M (1994). Organisms as ecosystem engineers. *Oikos* 69: 373–386.

Jones CG, Lawton JH & Shachak M (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957.

Karr JR & Freemark KE (1983). Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* 64: 1481–1494.

Keitt TH, Bjornstad ON, Dixon PM & Citron-Pousty S (2002). Accounting for spatial pattern when modeling organism-environment interactions. *Ecography* 25: 616–625.

Keitt TH & Fischer J (2006). Detection of scale-specific community dynamics using wavelets. *Ecology* 87: 2895–2904.

Keitt TH & Urban DL (2005). Scale-specific inference using wavelets. *Ecology* 86: 2497–2504.

Keitt TH, Urban DL & Milne BT (1997). Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1: 1–17.

Kerley GIH, Landman M, Kruger L, Owen-Smith N, Balfour D, De Boer WF, Gaylard A, Lindsay K & Slotow R (2008). Effects of elephants on ecosystems and biodiversity. *In* RJ Scholes & K Mennell, eds., *Elephant management: a scientific assessment for South Africa*, 329–369. Witwatersrand University Press, Johannesburg, South Africa.

Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A & De Ruiter PC (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213–217.

Kiel KA & Zabel JE (2008). Location, location, location: The 3L Approach to house price determination. *Journal of Housing Economics* 17: 175–190.

Kinahan AA, Inge-moller R, Bateman PW, Kotze A & Scantlebury M (2007a). Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana*). *Physiology and Behavior* 92: 560–565.

Kinahan AA, Pimm SL & van Aarde RJ (2007b). Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *Journal of Thermal Biology* 32: 47–58.

Kissling WD & Carl G (2008). Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography* 17: 59–71.

Klausmeier CA (1999). Regular and irregular patterns in semiarid vegetation. *Science* 284: 1826–1828.

Kleinbaum DG & Klein M (2005). *Survival analysis, a self learning text*. Springer, New York.

Kneitel JM & Chase JM (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7: 69–80.

Kohi EM, De Boer WF, Slot M, Van Wieren SE, Ferwerda JG, Grant RC, Heitkönig IMA, De Knegt HJ, Knox N, Van Langevelde F *et al.* (2010). Effects of simulated browsing on growth and leaf chemical properties in *Colophospermum mopane* saplings. *African Journal of Ecology* 48: 190–196.

Korner C (2007). The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* 22: 569–574.

Krebs CJ (2008). *The ecological world view*. CSIRO Publishing, Collingwood, Australia.

Kristan WB (2006). Sources and expectations for hierarchical structure in bird-habitat associations. *The Condor* 108: 5–12.

Kuhn I (2007). Incorporating spatial autocorrelation may invert observed patterns. *Diversity and Distributions* 13: 66–69.

Kumar L, Skidmore AK & Knowles E (1997). Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographical Information Science* 11: 475–497.

Kurzfeld-Zexer L, Wool D & Inbar M (2010). Modification of tree architecture by a gall-forming aphid. *Trees - Structure and Function* 24: 13–18.

Laliberté E, Paquette A, Legendre P & Bouchard A (2009). Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia* 159: 377–388.

Laws RM (1970). Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1–15.

Le Houérou HN (1980). *Browse in Africa: the current state of knowledge*. International Livestock Centre for Africa, Addis Ababa, Ethiopia.

Legendre P (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.

Legendre P, Borcard D & Peres-Neto PR (2005). Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75: 435–450.

Legendre P, Dale MRT, Fortin MJ, Gurevitch J, Hohn M & Myers D (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25: 601–615.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun IF & He F (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90: 663–674.

Lejeune O, Tlidi M & Couteron P (2002). Localized vegetation patches: A self-organized response to resource scarcity. *Physical Review E* 66: 010901/1–4.

Lennon JJ (2000). Red-shifts and red herrings in geographical ecology. *Ecography* 23: 101–113.

Levin SA (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* 73: 1943–1967.

Li H & Wu J (2004). Use and misuse of landscape indices. *Landscape Ecology* 19: 389–399.

Lima SL & Zollner PA (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11: 131–135.

Lindsay J (2006). TAS: Terrain Analysis System, version 2.0.9. http://www.uoguelph.ca/~hydrogeo/TAS/.

Lindsay JB (2005). The Terrain Analysis System: a tool for hydro-geomorphic applications. *Hydrological Processes* 19: 1123–1130.

Loarie SR, Aarde RJV & Pimm SL (2009a). Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation* 142: 3086–3098.

Loarie SR, van Aarde RJ & Pimm SL (2009b). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation* 142: 3099–3107.

Ludwig F, Dawson TE, Kroon H, Berendse F & Prins HHT (2003). Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia* 134: 293–300.

Ludwig F, De Kroon H & Prins HHT (2008). Impacts of savanna trees on forage quality

for a large African herbivore. *Oecologia* 155: 487–496.

Luskin RC (2008). Wouldn't it be nice ...? The automatic unbiasedness of OLS (and GLS). *Political Analysis* 16: 345–349.

Mac Nally R (2005). Scale and an organism-centric focus for studying interspecific interactions in landscapes. *In* JA Wiens & MR Moss, eds., *Issues and perspectives in landscape ecology*, 52–69. Cambridge University Press, New York.

Mackey BG & Lindenmayer DB (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography* 28: 1147–1166.

Mahalanobis PC (1936). On the generalised distance in statistics. *Proceedings National Institute of Science of India* 2: 49–55.

Makhabu SW, Skarpe C & Hytteborn H (2006). Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica* 30: 136–146.

Manly BFJ, McDonald LL & Thomas DL (1993). *Resource selection by animals. Statistical design and analysis for field studies*. Chapman and Hall, London.

Manning AD, Lindenmayer DB & Nix HA (2004). Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos* 104: 621–628.

Mayer AL & Cameron GN (2003). Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landscape and Urban Planning* 65: 201–217.

Mayor SJ, Schaefer JA, Schneider DC & Mahoney SP (2007). Spectrum of selection: new approaches to detecting the scale-dependent response to habitat. *Ecology* 88: 1634–1640.

Mayor SJ, Schaefer JA, Schneider DC & Mahoney SP (2009). The spatial structure of habitat selection: A caribou's-eye-view. *Acta Oecologica* 35: 253–260.

McComb K, Moss C, Durant SM, Baker L & Sayialel S (2001). Matriarchs as repositories of social knowledge in African elephants. *Science* 292: 491–494.

McIntire EJB & Fajardo A (2009). Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90: 46–56.

McIntyre NE & Wiens JA (1999a). How does habitat patch size affect animal movement? An experiment with darkling beetles. *Ecology* 80: 2261–2270.

McIntyre NE & Wiens JA (1999b). Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology* 14: 437–447.

McNaughton SJ (1983). Compensatory plant growth as a response to herbivory. *Oikos* 40: 329–336.

McNaughton SJ (1984). Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* 124: 863–886.

Meyer CB (2007). Does scale matter in predicting species distributions? Case study with the marbled murrelet. *Ecological Applications* 17: 1474–1483.

Milne G (1936). Normal erosion as a factor in soil profile development. *Nature* 138: 548–549.

Morales JM & Ellner SP (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* 83: 2240–2247.

Mueller T & Fagan WF (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* 117: 654–664.

Murwira A & Skidmore AK (2005). The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. *Landscape Ecology* 20: 217–234.

Mysterud A (1999). Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *Journal of Zoology* 247: 479–486.

Nathan R (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* 105: 19050–19051.

Nellemann C, Stein RM & Rutina LP (2002). Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. *Journal of Tropical Ecology* 18: 835–844.

Ngene SM, Skidmore AK, Van Gils H, Douglas-Hamilton I & Omondi P (2009). Elephant distribution around a volcanic shield dominated by a mosaic of forest and savanna (Marsabit, Kenya). *African Journal of Ecology* 47: 234–245.

Noy-Meir I (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.

Ntumi CP, Van Aarde RJ, Fairall N & De Boer WF (2005). Use of space and habitat by elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. *South African Journal of Wildlife Research* 35: 139–146.

Nunez-Farfan J, Fornoni J & Valverde PL (2007). The evolution of resistance and tolerance to herbivores. *Annual Review of Ecology, Evolution, and Systematics* 38: 541–566.

Oakes D (2001). Biometrika centenary: survival analysis. *Biometrika* 88: 99–142.

Ohashi K & Thomson JD (2005). Efficient harvesting of renewing resources. *Behavioral Ecology* 16: 592–605.

Ohashi K, Thomson JD & D'Souza D (2007). Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. *Behavioral Ecology* 18: 1–11.

Olden JD, Schooley RL, Monroe JB & Poff NL (2004). Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology* 73: 1190–1194.

O'Neill RV, DeAngelis D, Waide JB & Allen T (1986). *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, Princeton, New Jersey.

Openshaw S & Taylor PJ (1979). A million or so correlation coefficients, three experiments on the modifiable areal unit problem. *In* EN Wrigley, ed., *Statistical applications in the spatial science*, 127–144. Pion, London.

Openshaw S & Taylor PJ (1981). The modifiable areal unit problem. *In* N Wrigley & RJ Bennett, eds., *Quantitative geography: a British view*, 60–69. Routledge and Kegan Paul, London.

Ostfeld RS, Glass GE & Keesing F (2005). Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends in Ecology and Evolution* 20: 328–336.

Owen-Smith N (2002). Credible models for herbivore-vegetation systems: towards an ecology of equations. *South African Journal of Science* 98: 445–449.

Patlak C (1953). Random walk with persistence and external bias. *Bulletin of Mathematical Biophysics* 15: 311–338.

Patterson TA, Basson M, Bravington MV & Gunn JS (2009). Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology* 78: 1113–1123.

Patterson TA, Thomas L, Wilcox C, Ovaskainen O & Matthiopoulos J (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution* 23: 87–94.

Pebesma E (2004). Multivariable geostatistics in S: the gstat package. *Computers and*

Geosciences 30: 683–691.

Pebesma EJ (2007). The gstat package for R, R package version 0.9-42.

Pellew RA (1984). The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis tippelskirchi*). *Journal of Zoology* 202: 57–81.

Pellew RAP (1983). The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology* 21: 41–74.

Pelli DG & Tillman KA (2007). Parts, wholes, and context in reading: a triple dissociation. *PLoS ONE* 2: e680.

Peres-Neto PR, Legendre P, Dray S & Borcard D (2006). Variance partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614–2625.

Peterson DL & Parker VT (1998). *Ecological scale: theory and applications*. Columbia University Press, New York.

Pickett STA, Cadenasso ML & Benning TL (2003). Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. *In* JT Du Toit, HC Biggs & K Rogers, eds., *The Kruger experience: ecology and management of savanna heterogeneity*, 22–40. Island Press, Washington, DC.

Pickle L (2002). Spatial analysis of disease. *In* C Beam, ed., *Biostatistical applications in cancer research*, 113–150. Kluwer Academic Publishers, Tampa, FL.

Pinheiro J, Bates D, DebRoy S & Sarkar D (2008). nlme: Linear and nonlinear mixed effects models. R package version 3.1-90.

Pinter-Wollman N (2009). Spatial behaviour of translocated African elephants (*Loxodonta africana*) in a novel environment: using behaviour to inform conservation actions. *Behaviour* 146: 1171–1192.

Pinto N & Keitt TH (2008). Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos* 117: 1725–1731.

Possingham HP (1989). The distribution and abundance of resources encountered by a forager. *The American Naturalist* 133: 42–60.

Prins HHT & Olff H (1998). Species richness of African grazer assemblages: towards a functional explanation. *In* D Newberry, H Prins & N Brown, eds., *Dynamics of Tropical Communities*, 449–489. Blackwell Science, Oxford.

Prins HHT & Van der Jeugd HP (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* 81: 305–314.

Prins HHT, Ydenberg RC & Drent RH (1980). The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Botanica Neerlandica* 29: 585–596.

Pypker TG, Unsworth MH, Mix AC, Rugh W, Ocheltree T, Alstad K & Bond BJ (2007). Using nocturnal cold air drainage flow to monitor ecosystem processes in a complex terrain. *Ecological Applications* 17: 702–714.

R Development Core Team (2009). R: a language and environment for statistical computing. Version 2.8.1 R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rennó CD, Nobre AD, Cuartas LA, Soares JV, Hodnett MG, Tomasella J & Waterloo MJ (2008). HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sensing of Environment* 112: 3469–3481.

Rietkerk M, Boerlijst MC, Van Langevelde F, HilleRisLambers R, Van de Koppel J, Kumar L, Prins HHT & De Roos AM (2002a). Self-organization of vegetation in arid ecosystems. *American Naturalist* 160: 524–530.

Rietkerk M, Dekker SC, De Ruiter PC & Van de Koppel J (2004). Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305: 1926–1929.

Rietkerk M & Van de Koppel J (2008). Regular pattern formation in real ecosystems. *Trends in Ecology and Evolution* 23: 169–175.

Rietkerk M, Van de Koppel J, Kumar L, Van Langevelde F & Prins HHT (2002b). The ecology of scale. *Ecological Modelling* 149: 1–4.

Ripple WJ & Beschta RL (2007). Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138: 514–519.

Ripple WJ & Beschta RL (2008). Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation* 141: 1249–1256.

Rodriguez E, Morris CS & Belz JE (2006). A global assessment of the SRTM performance. *Photogrammetric Engineering and Remote Sensing* 72: 249–260.

Romero S, Campbell J, Nechols J & With K (2009). Movement behavior in response to landscape structure: the role of functional grain. *Landscape Ecology* 24: 39–51.

Rooney SM, Wolfe A & Hayden TJ (1998). Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review* 28: 89–98.

Roques KG, O'Connor TG & Watkinson AR (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268–280.

Rotenberry JT, Preston KL & Knick ST (2006). GIS-based niche modeling for mapping species' habitat. *Ecology* 87: 1458–1464.

Rushton G (2003). Public health, GIS and spatial analytic tools. *Annual Review of Public Health* 24: 43–56.

Rushton SP, Ormerod SJ & Kerby G (2004). New paradigms for modelling species distributions? *Journal of Applied Ecology* 41: 193–200.

Sala OE, Chapin I F S, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F *et al.* (2005). Determinants of woody cover in African savannas. *Nature* 438: 846–849.

Sankaran M, Ratman J & Hanan NP (2004). Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7: 480–490.

Scanlon TM, Caylor KK, Levin SA & Rodriguez-Iturbe I (2007). Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature* 449: 209–212.

Schabenberger O & Gotway CA (2005). *Statistical methods for spatial data analysis*. Chapman and Hall, Boca Raton, FL.

Schaefer JA & Mayor SJ (2007). Geostatistics reveal the scale of habitat selection. *Ecological Modelling* 209: 401–406.

Schenk HJ & Jackson RB (2002). Rooting depths, lateral root spreads and belowground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90: 480–494.

Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, Conde DA, Halpin PN, Joppa LN, McClellan CM & Clark JS (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* 11: 1338–1350.

Schlather M (2008). RandomFields: simulation and analysis of random fields, R package

version 1.3.35.

Schmidt J & Andrew R (2005). Multi-scale landform characterization. *Area* 37: 341–350.

Schmidt MH, Thies C, Nentwig W & Tscharntke T (2008). Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography* 35: 157–166.

Schneider DC (2001). The rise of the concept of scale in ecology. *BioScience* 51: 545–553.

Schofield G, Bishop CM, Katselidis KA, Dimopoulos P, Pantis JD & Hays GC (2009). Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology* 78: 14–21.

Scholes RJ & Archer S (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517–544.

Scholes RJ & Mennell KG (2008). *Elephant management, a scientific assessment for South Africa*. Wits University Press, Johannesburg.

Scholes RJ & Walker BH (1993). *An African savanna: synthesis of the Nyslvley study*. Cambridge University Press, Cambridge.

Schooley RL (2006). Spatial heterogeneity and characteristic scales of species-habitat relationships. *BioScience* 56: 533–537.

Segurado P, Araújo M & Kunin WE (2006). Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology* 43: 433–444.

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE & Swift DM (1987). Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *BioScience* 37: 789–799.

Shannon G, Druce DJ, Page BR, Eckhardt HC, Grant R & Slotow R (2008). The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology* 24: 281–289.

Shannon G, Page B, Duffy K & Slotow R (2006a). The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* 150: 344–354.

Shannon G, Page B, Slotow R & Duffy K (2006b). African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology* 41: 37–44.

Shannon G, Page BR, Duffy KJ & Slotow R (2010). The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation. *Austral Ecology* In press.

Shorrocks B (2007). *The biology of African savannahs*. Oxford University Press, Oxford.

Skarpe C & Hester A (2008). Plant traits, browsing and gazing herbivores, and vegetation dynamics. *In* IJ Gordon & HHT Prins, eds., *The ecology of browsing and grazing*, 9, 217–261. Springer, Berlin.

Skorupski P & Chittka L (2006). Animal cognition: an insect's sense of time? *Current Biology* 16: R851–R853.

Smallie JJ & O'Connor TG (2000). Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *African Journal of Ecology* 38: 352–359.

Smit IPJ, Grant CC & Devereux BJ (2007a). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation* 136: 85–99.

Smit IPJ, Grant CC & Whyte IJ (2007b). Elephants and water provision: what are the management links? *Diversity and Distributions* 13: 666–669.

Smit IPJ, Grant CC & Whyte IJ (2007c). Landscape-scale sexual segregation in the dry

season distribution and resource utilization of elephants in Kruger National Park, South Africa. *Diversity and Distributions* 13: 225–236.

Soberón J (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10: 1115–1123.

Soberón J & Nakamura M (2010). Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences* In Press.

Steffan-Dewenter I, Munzenberg U, Burger C, Thies C & Tscharntke T (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83: 1421–1432.

Stephens DW & Krebs JR (1986). *Foraging theory*. Princeton University Press, Princeton, N.J.

Stevens GC (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist* 140: 893–911.

Stokke S (1999). Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology* 77: 1723–1732.

Stokke S & Du Toit JT (2000). Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23: 70–80.

Stokke S & Du Toit JT (2002). Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology* 40: 360–371.

Switzer PV (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7: 533–555.

Szor G, Berteaux D & Gauthier G (2008). Finding the right home: distribution of food resources and terrain characteristics influence selection of denning sites and reproductive dens in arctic foxes. *Polar Biology* 31: 351–362.

Therneau TM (2009). survival: survival analysis, including penalised likelihood. R package version 2.35-7.

Thomas B, Holland JD & Minot EO (2008). Elephant (*Loxodonta africana*) home ranges in Sabi Sand Reserve and Kruger National Park: a five-year satellite tracking study. *PLoS ONE* 3: e3902–1–8.

Thorn JS, Nijman V, Smith D & Nekaris KAI (2009). Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Diversity and Distributions* 15: 289–298.

Tiefelsdorf M & Griffith DA (2007). Semiparametric filtering of spatial autocorrelation: the eigenvector approach. *Environment and Planning A* 39: 1193–1221.

Tilman D & Kareiva P (1997). *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey.

Tongway DJ & Ludwig JA (2005). Ecosystem function in heterogeneous landscapes. *In* GM Lovett, CG Jones, MG Turner & KC Weathers, eds., *Ecosystem function in heterogeneous landscapes*, 189–205. Springer, New York.

Treydte AC, Heitkönig IMA, Prins HHT & Ludwig F (2007). Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 197–205.

Treydte AC, Van Beeck FAL, Ludwig F & Heitkönig IMA (2008). Improved quality of beneath-canopy grass in South African savannas: Local and seasonal variation. *Journal of Vegetation Science* 19: 663–670.

Tsoar A, Allouche O, Steinitz O, Rotem D & Kadmon R (2007). A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions*

13: 397–405.

Turchin P (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72: 1253–1266.

Turchin P (1996). Fractal analyses of animal movement: a critique. *Ecology* 77: 2086–2090.

Turchin P (1998). *Quantitative analysis of movement. Measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Sunderland, Massachusetts.

Turner M, Gardner R & O'Neill R (2001). *Landscape ecology in theory and practice: pattern and process*. Springer, New York.

Turner MG (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171–197.

Turner MG, O'Neill RV, Gardner RH & Milne BT (1989). Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* 3: 153–162.

Van Aarde R, Ferreira S, Jackson T, Page B, De Beer Y, Gough K, Guldemond R, Junker J, Olivier P, Ott T *et al.* (2008). Elephant population biology and ecology. *In* RJ Scholes & K Mennell, eds., *Elephant management: a scientific assessment of South Africa*, 84–145. Witwatersrand University Press, Johannesburg, South Africa.

Van de Koppel J & Prins HHT (1998). The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology* 14: 565–576.

Van de Vijver CADM, Foley CAH & Olff H (1999). Changes in the woody component of an east African savanna during 25 years. *Journal of Tropical Ecology* 15: 545–564.

Van der Wal R, Van Wijnen H, Van Wieren S, Beucher O & Bos D (2000). On facilitation between herbivores: how Brent geese profit from brown hares. *Ecology* 81: 969–980.

Van Langevelde F (2000). Scale of habitat connectivity and colonization in fragmented nuthatch populations. *Ecography* 23: 614–622.

Van Langevelde F & Prins HHT (2008). Introduction to resource ecology. *In Resource ecology - Spatial and temporal dynamics of foraging*, 1–6. Springer, Dordrecht.

Van Langevelde F, Van de Vijver CADM, Kumar L, de Koppel J V, De Ridder N, Van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ *et al.* (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84: 337–350.

Van Nouhuys S & Kaartinen R (2008). A parasitoid wasp uses landmarks while monitoring potential resources. *Proceedings of the Royal Society B: Biological Sciences* 275: 377–385.

Van Teeffelen AJA & Ovaskainen O (2007). Can the cause of aggregation be inferred from species distributions? *Oikos* 116: 4–16.

Van Wesenbeeck K, Van de Koppel J, Herman M & Bouma J (2008). Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems? *Oikos* 117: 159–159.

Van Wijk MT & Rodriguez-Iturbe I (2002). Tree-grass competition in space and time: insights from a simple cellular automata model based on ecohydrological dynamics. *Water Resources Research* 38: 18/1–18/15.

VanDerWal J, Shoo L, Johnson C & Williams S (2009). Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist* 174: 282–291.

Venter FJ, Scholes RJ & Eckhardt HC (2003). The abiotic template and its associated vegetation pattern. *In* JT Du Toit, HC Biggs & K Rogers, eds., *The Kruger experience: ecology and management of savanna heterogeneity*, 83–129. Island Press, Washington,

DC.

Vilchis LI, Ballance LT & Fiedler PC (2006). Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. *Marine Ecology Progress Series* 315: 279–292.

Viswanathan GM, Buldyrev SV, Havlin S, Da Luz MGE, Raposo EP & Stanley HE (1999). Optimizing the success of random searches. *Nature* 401: 911–914.

Wagner HH (2004). Direct multi-scale ordination with canonical correspondence analysis. *Ecology* 85: 342–351.

Wagner HH & Fortin MJ (2005). Spatial analysis of landscapes: concepts and statistics. *Ecology* 86: 1975–1987.

Walker BH, Ludwig D, Holling CS & Peterman RM (1981). Stability of semi-arid savana grazing systems. *Journal of Ecology* 69: 473–498.

Walker BH & Noy-Meir I (1982). Aspects of stability and resilience of savanna ecosystems. *In* BJ Huntley & BH Walker, eds., *Ecology of tropical savannas*, 555–590. Springer, Berlin.

Wall J, Douglas-Hamilton I & Vollrath F (2006). Elephants avoid costly mountaineering. *Current Biology* 16: R527–R529.

Wallar LA (2009). Detection of clustering in spatial data. *In* AS Fotheringham & PA Rogerson, eds., *The SAGE handbook of spatial analysis*, 299–320. SAGE Publications Ltd, Los Angeles.

Walter H (1971). *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh.

Wang T (2009). *Observing giant panda habitat and forage abundance from space*. Ph.D. thesis, PhD thesis. International Institute for Geo-Information Science and Earth Observation (ITC).

Wang YH, Yang KC, Bridgman C & Lin LK (2008). Habitat suitability modelling to correlate gene flow with landscape connectivity. *Landscape Ecology* 23: 989–1000.

Ward MD & Gleditsch KS (2002). Location, location, location: an MCMC approach to modeling the spatial context of war and peace. *Political Analysis* 10: 244–260.

Watts DP (1998). Long-term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 2. Reuse of foraging areas in relation to resource abundance, quality, and depletion. *International Journal of Primatology* 19: 681–702.

Weber GE & Jeltsch F (2000). Long-term impacts of livestock herbivory on herbaceous and woody vegetation in semiarid savannas. *Basic and Applied Ecology* 1: 13–23.

Wellnitz TA, Poff NL, Cosyleón G & Steury B (2001). Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. *Landscape Ecology* 16: 111–120.

Weltzin JF & McPherson GR (1997). Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* 112: 156–164.

Western D & Maitumo D (2004). Woodland loss and restoration in a savanna park: a 20-year experiment. *African Journal of Ecology* 42: 111–121.

Wheatley M & Johnson C (2009). Factors limiting our understanding of ecological scale. *Ecological Complexity* 6: 150–159.

White EP & Brown JH (2005). The template: patterns and processes of spatial variation. *In* GM Lovett, CG Jones, MG Turner & KC Weathers, eds., *Ecosystem function in heterogeneous landscapes*, 31–47. Springer, New York.

Wiens JA (1989). Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

Wiens JA (2002). Predicting species occurrences: progress, problems, and prospects. *In* JM Scott, PJ Heglund, ML Morrison, JB Haufler, MG Raphael, WA Wall & FB Samson, eds., *Predicting species occurrences: issues of accuracy and scale*, 739–749. Island Press, Covelo, CA.

Wiens JJ & Donoghue MJ (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* 19: 639–644.

Williams NM & Thomson JD (1998). Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants. *Behavioral Ecology* 9: 612–621.

Witkowski ETF & O'Connor TG (1996). Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. *Plant Ecology* 124: 9–23.

Wittemyer G, Getz W, Vollrath F & Douglas-Hamilton I (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology* 61: 1919–1931.

Wittemyer G & Getz WM (2007). Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Animal Behaviour* 73: 671–681.

Wittemyer G, Polansky L, Douglas-Hamilton I & Getz WM (2008). Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *Proceedings of the National Academy of Sciences* 105: 19108–19113.

Wolf M, Frair J, Merrill E & Turchin P (2009). The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* 32: 401–410.

Wong D (2009). The Modifiable Areal Unit Problem (MAUP). *In* AS Fotheringham & PA Rogerson, eds., *The SAGE handbook of spatial analysis*, 105–123. SAGE Publications Ltd, Los Angeles.

Wood J (2009a). Geomorphometry in LandSerf. *In* T Hengl & H Reuter, eds., *Geomorphometry - concepts, software, applications*, 333–349. Elsevier, Amsterdam.

Wood J (2009b). LandSerf, version 2.3. http://www.landserf.org.

Woolnough AP & Du Toit JT (2001). Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* 129: 585–590.

Wu J (2007). Scale and scaling: a cross-disciplinary perspective. *In* J Wu & RJ Hobbs, eds., *Key topics in landscape ecology*, 115–136. Cambridge University Press, Cambridge.

Wu J & Li H (2006). Concepts of scale and scaling. *In* J Wu, KB Jones, H Li & OL Loucks, eds., *Scaling and u ncertainty analysis in ecology. Methods and applications*, 3–15. Springer, Dordrecht, The Netherlands.

Wu J, Li H, Jones B & Loucks O (2006). Scaling with known uncertainty: a synthesis. *In* J Wu, KB Jones, H Li & OL Loucks, eds., *Scaling and u ncertainty analysis in ecology. Methods and applications*, 329–346. Springer, Dordrecht, The Netherlands.

Wu J, Shen W, Sun W & Tueller PT (2002). Empirical patterns of the effects of changing scale on landscape metrics. *Landscape Ecology* 17: 761–782.

Zeng Z, Skidmore AK, Song Y, Wang T & Gong H (2008). Seasonal altitudinal movements of golden takin in the Qinling Mountains of China. *Journal of Wildlife Management* 72: 611–617.

Zollner PA & Lima SL (1999). Search strategies for landscape-level interpatch movements. *Ecology* 80: 1019–1030.

Summary

*T*he interactions between organisms and their environment are at the heart of ecological research, and it is the central theme in this thesis. These interactions influence the movement of organisms, ultimately determining the spatial distribution of populations. Hence, the way organisms respond to environmental heterogeneity is of major importance for understanding ecological phenomena. However, organisms not only respond to environmental heterogeneity: they actively modify their environment and influence that of other species.

Although the way organisms interact with their environment is central to ecology from its very beginning, it has for a long time been analysed spatially and temporarally inexplicit. Yet recently, an increasing emphasis has been placed on spatial processes in ecological systems, as the potential effects of the landscape surrounding a site ("environmental context") on organisms at the site has been appreciated more fully. Moreover, the influence of past events or processes on present-day ecological phenomena is increasingly being recognized.

Furthermore, the issue of scale has featured as a central topic over the past decades, since it is present in every facet of ecological research. When studying species-environment relationships, one deals with at least three components of scale: (1) the scales of environmental variation, (2) the scale at which species respond to this variation, and (3) the scales of data collection and analysis. The processes creating environmental heterogeneity operate over a wide array of spatial and temporal scales. Likewise, the processes that determine the response of organisms to this heterogeneity also vary as function of scale. Hence, analysing species-environment relationships at inappropriate scales may misconstrue the processes responsible for creating the observed patterns.

In this thesis, I focus on the interactions between organisms and their environment, focussing on both the response of organisms to environmental heterogeneity as well as their role in creating environmental heterogeneity. I do this at different spatial scales, and over different time frames. Moreover, I focus on the importance of processes and factors that are "beyond the here and now", as is the main title of this thesis. Namely, beyond *here* is *there*, and beyond *now* are *past* and *future*: the importance of *there* must be recognized for understanding ecological phenomena *here*, but also the importance of the *past* in understanding the *present*. Together, these issues influence our ability to predict the *future*. In summary, the central question dealt with in this thesis is how spatial-temporal context influences the relationships between organisms and their environment, and at what scale(s) this context is important.

In Chapter 2, I investigate how environmental heterogeneity, created by topographic processes, influences the movement and distribution of African elephants (*Loxodonta africana*) in Kruger National Park (KNP), South Africa. Topography usually has a severe

influence on landscape heterogeneity, through influencing broad climatic gradients as well as local gradients in soil moisture and nutrients. Especially in savanna ecosystems with intermediate rainfall, undulating terrain gives rise to pronounced topo-edaphic patterning, because rain falling on an undulation gravitates from the top, via the slopes, to the bottom, carrying with it soluble material and soil particles. The series of undulations, together with the associated soil and vegetation, are known as "catenas". In KNP, relatively open vegetation on sandy soils can be found at the crests of catenas, and more dense vegetation on clay soils containing more nutrients and water is found in the valleys.

Valleys and low-lying parts of the catena therefore often have vegetation of higher quality and quantity, remaining green for longer in the dry season, therefore being important for herbivores during dry periods. Furthermore, the more densely vegetated lower parts of the catena may supply shade to heat sensitive animals compared to the more open vegetation on the crest of catenas. The vegetation in the lower parts of the catena may thus be important to elephants, that may face physiological problems of dissipating heat during spells of extremely high ambient temperatures. Chapter 2 shows that the elephants move up and down the catenary gradient in cyclic rhythms that follow the seasonal patterns of rainfall and circadian patterns of solar radiation and temperature. In the dry season, and during midday, the elephants preferred to be predominantly at the lower parts of the catena, while being distributed indifferently over the catenary gradient in the wet season and during the night. Hence, local topography is important in savanna ecosystems, because it interacts with climate to mediate the distribution of nutrients and moisture over the landscape, influencing the patterning and productivity of vegetation, and affecting the distribution of large herbivores.

Then, in Chapter 3, I ask the question whether and through which mechanisms herbivores can induce spatial patterning in savanna vegetation. Using simulation modelling, I test the assumptions that herbivore-vegetation feedbacks as well as the influence of environmental context are necessary for herbivores to induce spatial vegetation patterning. The model shows that herbivores can induce vegetation patterning only when two key assumptions are fulfilled. First, they have to increase the attractiveness of a site while foraging so that they will revisit this site, e.g., through an increased availability or quality of forage. The model shows that grazers are able to maintain permanent grazing lawns through a positive feedback loop (grazing-regrowth-regrazing) that generates enhanced productivity in a short sward, with vegetation that is of higher quality. Browsers, however, suppress the recruitment of trees into the mature stage, thereby increasing the portion of the tree canopy that is within reach of the browsers. Second, foraging should be spatially explicit, e.g., when foraging at a site influences vegetation at larger spatial scales or when vegetation at larger spatial scales influences the selection and utilisation of a site. However, the model shows that the pre-existing spatial pattern in vegetation influences the process of vegetation patterning through herbivory, although this influence decreases when the heterogeneity and scale of patchiness of the initial vegetation decreases. Moreover, vegetation patterning only occurs at intermediate herbivore densities, as high herbivore densities lead to homogenisation of the vegetation.

Thus, positive plant-herbivore interactions may stimulate herbivores to frequently visit previously visited areas, leading to site fidelity. In Chapter 4, I therefore analyze the patterns of site fidelity by elephants in KNP by analyzing how visits to specific sites in the landscape are related to visits of those sites in the past. I specifically focus on the

influence of the two main resources for elephants, namely vegetation and water, on the patterns of site revisitation. Moreover, because surface water availability varies seasonally, and because vegetation growth is dependent on seasonal rainfall patterns, I analyze the patterns of site revisitation in relation to these resources taking into account seasonality in rainfall. The results show that elephants do not avoid previously utilized areas but seem to exhibit the tendency to return to sites already visited above what can be expected from random movements alone. Furthermore, the patterns of site fidelity were not solely determined by the preference for certain sites independent of past experience, as some sites were often visited but not much revisited and others not much visited but often revisited. The elephants were more likely to be site-faithful when surface water became scarce, i.e., during the dry season, and in areas close to water. In contrast, the elephants were generally less site-faithful in areas with high tree cover. However, this was not the case for female elephants concerning sites close to water, probably because these areas provide not only water, but also shelter and abundant forage that is of high quality. Although we did not find strong overall differences between male and female elephants, the female elephants seemingly timed revisits to specific sites taking into account the environmental and climatic conditions. This might be due to the more stringent requirements regarding the quality and accessibility of forage regarding the female elephants and the young individuals within family herds, which we hypothesize to increase the incentive to consume the regrowth of vegetation previously been utilized. Overall, Chapter 4 shows that familiarity with specific sites has a large influence on the movement of elephants.

The following two chapters (Chapter 5 and 6) focus on the influence of the spatial scale of analysis on the quantification and predictability of species distributions. Chapter 5 highlights the interplay between spatial autocorrelation in the residuals of regression methods and the spatial scaling of species-environment relationships. Using a hypothetical species in an artificial landscape, this chapter shows the consequences of a scale mismatch on such analyses and the interpretation thereof. Namely, Chapter 5 shows that a mismatch between the scale of analysis and the scale of a species' response to its environment leads to a decrease in the portion of variation explained by environmental predictors. Moreover, it results in residual spatial autocorrelation (RSA) and biased regression coefficients. This bias stems from error-predictor dependencies that are due to the scale mismatch. The magnitude of the error-predictor correlation depends on the interaction between the scale of landscape heterogeneity and the scale of a species' response to this heterogeneity. Because error-predictor correlations are difficult to diagnose, this is a serious problem for spatial analyses of species distributions. However, Chapter 5 shows that explicitly considering scale effects on RSA can reveal the scale at which a species responds to its environment. This is important, because the estimation of species-environment relationships using spatial regression methods is shown in Chapter 5 to be erroneous in case of a scale mismatch, leading to spurious conclusions when scaling issues are not explicitly considered. Thus, this chapter highlights the importance of examining the appropriateness of the spatial scales used in analyses, since scale mismatches affect the rigour of statistical analyses and thereby the ability to understand the processes underlying spatial patterning in ecological phenomena.

Therefore, in Chapter 6, I analyze the broad-scale distribution pattern of elephants in KNP, focusing on the spatial scale at which elephants respond to their main resources, i.e., water and forage. This chapter shows that the inclusion of environmental context at the

appropriate spatial scale improves the quantification of habitat selection, and increases the predictive capacity of habitat suitability models. The elephants responded to their environment in a scale-dependent manner, with forage characteristics driving habitat selection at coarse spatial scales, and surface water at fine spatial scales. The elephants were found to exhibit sexual segregation regarding habitat selection, mainly in relation to their response to vegetation and topography. Namely, the male elephants preferred areas with high tree cover but avoided areas with much herbaceous biomass, whereas this pattern was reversed for the female elephants.

Chapter 7, finally, synthesises the conclusions that can be drawn from the preceding chapters and puts the issues addressed in a broader context of species-environment relationships. In summary, this thesis shows that herbivores can create reciprocal spatial patterns in vegetation and herbivore distribution, even in the absence of any underlying spatial heterogeneity, due to positive plant-herbivore interactions. In addition, physical processes related to for example climate and topography create distinct spatial and temporal heterogeneity in the resources that herbivores require, as well as the abiotic conditions that influence the their physiology. The scales of environmental heterogeneity may determine the scales at which species respond to their environment, but their response to environmental variation may also be species specific. Either way, analysing species-environment relationships at inappropriate scales most likely misconstrue the quantification and predictability of species-environment. Hence, a major challenge in ecology is to appropriately characterize the scales that are relevant to the organisms under study, and then to accurately measure their response to environmental heterogeneity at those scales. Explicitly considering the influence of spatial-temporal scale and context on the interactions between organisms and their environment opens exciting avenues for increasing our understanding of the processes determining the distribution and abundance of organisms.

Samenvatting

$\mathscr{D}$e interacties tussen organismen en hun omgeving vormen het hart van ecologisch onderzoek; het is ook het centrale thema van dit proefschrift. Deze interacties beïnvloeden de beweging van organismen, hetgeen uiteindelijk de ruimtelijke verspreiding van populaties bepaald. De mannier waarop organismen op heterogeniteit in de omgeving reageren is daardoor uiterst belangrijk voor het begrijpen van ecologische fenomenen. Echter, organismen reageren niet alleen op heterogeniteit in de omgeving: zij kunnen ook actief hun omgeving veranderen, en daarmee dat van andere soorten.

Hoewel de interacties tussen organismen en hun omgeving centraal staan in de ecologie, zijn ecologische analyses vaak uitgevoerd zonder ruimte en tijd expliciet mee te nemen. Recentelijk wordt er echter een steeds toenemende nadruk gelegd op de rol van ruimtelijke processen in ecologische systemen, en wordt de potentiële invloed van het landschap in de nabijheid van een locatie ("landschappelijke context") op organismen op die locatie steeds meer gewaardeerd. Bovendien wordt de invloed van gebeurtenissen of processen in het verleden steeds meer erkent als belangrijk voor ecologische fenomenen vandaag de dag.

Daarnaast is de kwestie van schaal een steeds centralere rol gaan spelen, omdat het aanwezig is in elk facet van ecologisch onderzoek. Bij het bestuderen van de relaties tussen soorten en hun omgeving heeft men te maken met minimaal drie componenten van schaal: (1) de schalen van ruimtelijke variatie in de omgeving, (2) de schalen waarop soorten reageren op deze variatie, en (3) de schalen waarop data wordt verzameld of geanalyseerd. De processen die omgevingsvariatie creëren opereren over een breed scala aan temporele en ruimtelijke schalen. De processen die de respons van organismen op deze variatie bepalen variëren eveneens over vele schalen. Analysen van de relaties tussen soorten en hun omgeving kunnen daardoor de processen die verantwoordelijk zijn voor het creëren van de geobserveerde patronen misduiden als deze op verkeerde schalen uitgevoerd worden.

In dit proefschrift focus ik op de relaties tussen organismen en hun omgeving, zowel de respons van organismen op ruimtelijke heterogeniteit alsook de rol van organismen in het creëren van ruimtelijke heterogeniteit. Ik doe dit op verschillende ruimtelijke schalen, en over verschillende tijdsspannen. Ik focus met name op de belangrijkheid van processen of factoren die "achter het hier en nu" liggen, zoals de hoofd titel van dit proefschrift luidt. Namelijk, achter het *hier* ligt het *daar,* en achter het *nu* liggen *verleden* en *toekomst*: de belangrijkheid van het *daar* moet worden herkend om ecologische fenomenen *hier* te kunnen begrijpen, maar ook het *verleden* is van belang om het *heden* te kunnen begrijpen. Gezamenlijk beïnvloeden deze kwesties onze capaciteit om de *toekomst* te kunnen voorspellen. Samenvattend is centrale vraag in dit proefschrift hoe de ruimte-tijd context de relaties tussen organismen en hun omgeving beïnvloed, en

op welke schaal (schalen) deze context belangrijk is.

In hoofdstuk 2 bekijk ik hoe omgevingsvariatie, gecreëerd door topografische processen, de beweging en verspreiding van Afrikaanse olifanten (*Loxodonta africana*) in Kruger Nationaal Park (KNP), Zuid Afrika, beïnvloed. Deze invloed heb ik geanalyseerd op verschillende tijdschalen, van patronen binnen een dag tot patronen over de seizoenen, en op verschillende ruimtelijke schalen, van kleinschalig topografisch reliëf tot grootschalig reliëf. Topografie heeft normaal gesproken een grote invloed op de landschappelijke heterogeniteit, door bijvoorbeeld het beïnvloeden van grootschalige klimatologische gradiënten alsook kleinschalige gradiënten in bodemvochtigheid en bodemnutriënten. Zeker in savanne ecosystemen met gemiddelde regenval geeft een golvend terrein aanleiding tot de vorming van uitgesproken topografische bodem patronen, omdat regen dat op een heuvel valt naar de vallei afstroomt en oplosbare nutriënten en bodemdeeltjes met zich mee neemt. Een golving in het landschap, samen met het geassocieerde bodem en vegetatieprofiel, staat bekend als een "catena". In KNP, relatief open vegetatie op zandgrond is te vinden op de top van een catena, en meer dichtbegroeide vegetatie op kleihoudende grond dat meer nutriënten en water bevat is te vinden in de valleien.

Valleien en laaggelegen delen van de catena hebben daarom vaak vegetatie dat van hogere kwaliteit en kwantiteit is, en het blijft langer groen gedurende het droge seizoen, hetgeen deze delen van de catena belangrijk maakt voor herbivoren tijdens het droge seizoen. Bovendien bieden de meer dichtbegroeide laaggelegen delen van de catena schaduw aan hittegevoelige dieren vergeleken met de meer open vegetatie op de hooggelegen delen van de catena. De vegetatie in de laaggelegen delen van de catena kan dus belangrijk zijn voor olifanten, welke fysiologische problemen kunnen hebben met het kwijtraken van lichaamswarmte tijdens perioden van extreme hitte. Hoofdstuk 2 laat zien dat de olifanten zich op en neer de catena gradiënt begeven in ritmische cycli die overeenkomen met de seizoenale patronen van regenval en de dagelijkse patronen van zonlicht en temperatuur. In het droge seizoen en midden op de dag zijn de olifanten voornamelijk te vinden in de laag gelegen delen van de catena, terwijl ze random over de catena zijn verdeeld in het natte seizoen en gedurende de nacht. Lokale topografie is daarom belangrijk voor savanne ecosystemen, omdat het de herverdeling van nutriënten en water over het landschap beïnvloed, wat daarmee de ruimtelijke verdeling van vegetatie patronen en productiviteit beïnvloed, en zodoende invloed uitoefent op de verdeling van grote herbivoren over het landschap.

In hoofdstuk 3 stel ik vervolgens de vraag óf, en zo ja door welke mechanismen, herbivoren ruimtelijke patronen in savanne vegetatie kunnen veroorzaken. Gebruik makende van simulatie modellering test ik de aannames dat herbivoor-vegetatie terugkoppelingen alsook de invloed van ruimtelijke context nodig zijn als voorwaarden voor herbivoren om vegetatie patronen te kunnen veroorzaken. Het model laat zien dat herbivoren alleen ruimtelijke vegetatie patronen kunnen creëren als aan deze twee voorwaarden is voldaan. Ten eerste moeten herbivoren tijdens het foerageren de aantrekkelijkheid van een locatie verhogen zodat zij deze locatie opnieuw zullen bezoeken, bv. door het verhogen van de hoeveelheid of kwaliteit van de vegetatie. Het model laat zien dat grazers in staat zijn permanente grasvlakten kunnen onderhouden door een positieve terugkoppeling (grazen-hergroei-grazen) die een verhoogde productiviteit van een korte grasvlakte genereert, met vegetatie dat van hoge kwaliteit is. Bladeters, echter, vertragen of blokkeren de ontwikkeling van bomen richting volgroeiing, en verhogen daarbij het

aandeel van de boomkroon dat binnen het bereik van de bladeters is. Ten tweede moet het forageerproces ruimtelijk expliciet zijn, bv. als forageren op een locatie de vegetatie rondom die locatie beïnvloed, of als de vegetatie rondom de locatie de aantrekkelijkheid van die locatie beïnvloed. Echter, de vorming van vegetatiepatronen komt alleen voor bij gemiddelde herbivoor dichtheden, omdat een hoge herbivoor dichtheid leidt to homogenisatie van de vegetatie. Bovendien laat het model zien dat de aanwezigheid van initiële vegetatiepatronen de vorming van vegetatiepatronen door herbivoren beïnvloed, hoewel deze invloed minder wordt als de initiële heterogeniteit en de schaal van de initiële heterogeniteit kleiner worden.

Dus, positieve herbivoor-plant terugkoppelingen kunnen een stimulans zijn voor herbivoren om trouw te zijn aan locaties en deze vaak te (her)bezoeken. In hoofdstuk 4 analyseer ik daarom de patronen van locatiegetrouwheid van olifanten in KNP door te analyseren hoe visitaties van specifieke locaties in het landschap gerelateerd zijn aan visitaties van die locaties in het verleden. In het bijzonder focus ik op de invloed van twee belangrijke hulpbronnen voor olifanten, namelijk vegetatie en water, op de patronen van hun locatiegetrouwheid. Omdat de beschikbaarheid van oppervlaktewater seizoensafhankelijk is, alsook de groei van vegetatie, analyseer ik de patronen van locatie herbezoek in relatie tot deze twee componenten rekening houdende met seizoensafhankelijke regenval. De resultaten laten zien dat de olifanten voorheen bezochte locaties niet vermijden, maar juist vaker lijken te bezoeken dan men kan verwachten op basis van willekeurige beweging. Bovendien zijn de patronen van locatiegetrouwheid niet alleen gerelateerd aan de voorkeur voor specifieke locaties, omdat sommige locaties vaak werden bezocht maar niet vaak werden herbezocht, terwijl andere locaties niet vaak werden bezocht maar wel relatief vaak herbezocht. De olifanten waren meer getrouw aan locaties als oppervlaktewater schaars werd, namelijk in het droge seizoen, en in gebieden dicht bij water. Daarentegen waren de olifanten minder getrouw aan locaties in gebieden met een hoge boombedekking. Echter, dit was niet het geval voor vrouwelijke olifanten in locaties dicht bij water, waarschijnlijk omdat deze locaties niet alleen water bieden, maar ook beschutting en veel vegetatie van hoge kwaliteit. Ook al vond ik geen sterke verschillen tussen mannetjes en vrouwtjes olifanten, de vrouwtjes lijken de her-visitaties naar bepaalde locaties te timen als functie van landschap- en weer- omstandigheden Dit kan komen door de strikte eisen aangaande de kwaliteit en beschikbaarheid van vegetatie van vrouwelijke en jonge olifanten, hetgeen hen kan aansporen de hergroei van vegetatie beter te benutten dan mannetjes olifanten. Hoofdstuk 4 laat dus zien dat vertrouwdheid met specifieke locaties een grote invloed heeft op de beweging van olifanten.

Hoofdstukken 5 en 6 focussen op de invloed van de ruimtelijke schaal van analyse op de beschrijving en voorspelbaarheid van habitat selectie door organismen. Hoofdstuk 5 laat de wisselwerking tussen ruimtelijke autocorrelatie in de residuen van regressie modellen en het ruimtelijke schalen van soort-omgeving relaties zien. Gebruikmakende van een hypothetisch soort en een kunstmatig landschap laat dit hoofdstuk de consequenties zien van analysen op een verkeerde schaal. Namelijk, hoofdstuk 5 laat zien dat een schaal van analyse die niet overeenkomt met de schaal waarop een soort reageert op zijn omgeving leidt tot een verkleining van het deel van variatie dat verklaard kan worden door omgevingsvariabelen. Bovendien zorgt een verkeerde schaal van analyse voor ruimtelijke autocorrelatie in de residuen van regressie modellen (RSA), alsook een afwijkende schatting van regressie coëfficiënten. Deze afwijking komt door fout-voorspeller afhankelijkheid in regressie analysen als gevolg van het gebruik van een verkeerde schaal.

De sterkte van deze afhankelijkheid hangt af van de interactie tussen de schaal van landschappelijke heterogeniteit en de schaal waarop een soort reageert op deze heterogeniteit. Omdat deze afhankelijkheid moeilijk te diagnosticeren valt is dit een ernstig probleem voor ruimtelijke analysen. Echter, hoofdstuk 5 laat zien dat het expliciet rekening houden met de invloed van schaal op RSA de schaal kan onthullen waarop een soort op zijn omgeving reageert. Dit is belangrijk, omdat het schatten van soort-omgeving relaties met behulp van ruimtelijke regressiemethoden abusievelijk is als er sprake is van een verkeerde schaal, wat leidt tot verkeerde conclusies als schaal effecten niet worden overwogen. Dus, dit hoofdstuk benadrukt de belangrijkheid van het inspecteren van de gepastheid van de ruimtelijke schalen van analyse, omdat een verkeerde schaal de statistische analyse en daarmee de mogelijkheid tot het begrijpen van processen in ecologische fenomenen negatief beïnvloed.

Daarom analyseer ik in hoofdstuk 6 de verspreiding van olifanten in KNP, focussende op de ruimtelijke schaal waarop de olifanten reageren op hun voornaamste hulpbronnen, namelijk water en vegetatie. Dit hoofdstuk laat zien dat de inachtneming van landschappelijke context op de juiste ruimtelijke schaal de beschrijving van habitat selectie verbeterd en de voorspelbaarheid van habitat selectie modellen vergroot. De olifanten reageerden op hun omgeving op een schaalafhankelijke mannier, waarbij de vegetatie habitat selectie op een grote schaal beïnvloedde, en oppervlaktewater invloed uitoefende op een kleine schaal. De olifanten vertoonden sexuele segregatie betreffende habitat selectie, vooral in relatie tot hun reactie op de vegetatie en topografie. De mannetjes olifanten prefereerden namelijk gebieden met een hoge boombedekking maar vermeden gebieden met veel grasvegetatie, terwijl dit patroon omgekeerd was voor de vrouwtjes olifanten.

Tot slot synthetiseert hoofdstuk 7 de conclusies die getrokken kunnen worden uit de voorgaande hoofdstukken en plaatst de kwesties uit dit proefschrift in de bredere context van soort-omgeving relaties. Samenvattend laat dit proefschrift zien dat herbivoren wederkerige ruimtelijke patronen in vegetatie en herbivoor verspreiding kunnen creëren, zelfs in de afwezigheid van enige vorm van ruimtelijke variatie, door positieve plant-herbivoor terugkoppelingen. Bovendien kunnen fysieke processen gerelateerd aan bijvoorbeeld klimaat en topografie duidelijke ruimtelijke en temporele variatie in de water- en voedselbronnen voor herbivoren creëren, alsook variatie in de abiotische factoren die hun fysiologie beïnvloeden. De schalen van omgevingsvariatie kunnen de schalen bepalen waarop organismen moeten reageren op hun omgeving, maar de schaal van deze reactie kan ook soortspecifiek zijn. In beide gevallen leidt de analyse van soort-omgeving relaties tot verkeerde conclusies en een lagere voorspelbaarheid als de analyse niet op de goede schaal plaats vindt. Een grote uitdaging voor ecologisch onderzoek is daarom het karakteriseren van de relevante schalen voor de organismen die bestudeerd worden, om vervolgens hun reactie op omgevingsvariatie goed te kunnen meten. Expliciet rekening houden met de invloed van ruimtelijke en temporele schaal en context op de interacties tussen organismen en hun omgeving opent enerverende mogelijkheden voor het vergroten van ons begrip van de processen die de ruimtelijke verspreiding van organismen bepalen.

Opsomming

$\mathcal{D}$ ie wisselwerking tussen organismes en hul omgewing vorm die basis van ekologiese navorsing en is die sentrale tema van hierdie tesis. Hierdie interaksies beïnvloed die beweging van organismes, en bepaal uiteindelik die ruimtelike verspreiding van bevolkings. Die wyse waarop organismes reageer op omgewings-heterogeniteit is daarom van groot belang om ekologiese verskynsels te verklaar. Organismes reageer egter nie net op omgewings heterogeniteit nie, maar verander op sigself hul omgewing en beïnvloed dié van ander soorte.

Alhoewel die wyse van wisselwerking tussen organismes en hul omgewing sentraal staan in ekologie, was dit vir 'n lang periode nie eksplisiet geanaliseer in terme van ruimte en tyd nie. Onlangs is egter klem gelê op ruimtelike prosesse in ekologiese sisteme na gelang die potensiële effek van die omliggende landskap rondom 'n plek ("omgewings-konteks") op die organisme van daardie plek meer na waarde geskat word. Die invloed van gebeure of prosesse in die verlede op hedendaagse ekologiese verskynsels word toenemend erken.

Ook het die kwessie van skaal as 'n sentrale onderwerp die laaste dekades uit gestaan, omrede dit in elke faset van ekologiese navorsing teenwoordig is. Wanneer spesie-omgewings verwantskappe bestudeer word, het 'n mens met ten minste met drie onderafdelings van skaal te doen: (1) die skaal van omgewings variasie, (2) die skaal waar spesies reageer op hierdie variasie, en (3) die skaal waarmee inligting versamel en verwerk word. Die prosesse wat omgewings-heterogeniteit skep werk oor 'n wye reeks ruimtelike en tyds skale. Net so verander die prosesse wat die reaksie van organismes op heterogeniteit bepaal, ook na gelang van skaal. Daarom kan die verwerking van spesie-omgewings verwantskappe by ontoepaslike skale 'n verkeerde beeld skep van die prosesse verantwoordelik vir die skepping van waargenome patrone.

In hierdie tesis fokus ek op die wisselwerkings tussen organismes en hul omgewing vir beide die reaksie van organismes op omgewings-heterogeniteit asook hul rol in die skepping van omgewings-heterogeniteit. Ek doen dit vir verskillende ruimtelike skale en oor verskillende tydvakke. Ek fokus voorts op die belangrikheid van prosesse en faktore wat "bo die hier en nou" is, soos die titel van hierdie tesis lui. Naamlik, verby *hier* is *daar*, en na *nou* is *verlede* of *toekoms*: die belangrikheid van *daar* moet erken word om ekologiese verskynsels *hier* te verstaan, asook die belangrikheid van die *verlede* om die *hede* te verstaan. Te same beïnvloed hierdie vraagstukke ons vermoë om die *toekoms* te voorspel. Ter opsomming, die sentrale vraag wat behandel word in hierdie tesis behels hoe die ruimte-tyd konteks die wisselwerking tussen organismes en hul omgewing beïnvloed, en by watter skaal hierdie konteks belangrik is.

In Hoofstuk 2 ondersoek ek hoe omgewings-heterogeniteit, geskep deur topografiese prosesse, die bewegings en verspreiding van Afrika olifante (*Loxodonta africana*) in die

Kruger Nasionale Park in Suid Afrika beïnvloed. Topografie het gewoonlik 'n opmerklike invloed op landskap-heterogeniteit beide op breë klimaats-gradiënte asook lokale gradiënte in grondvogtigheid en voedingstowwe. In savanna ekosisteme met gemiddelde reënval en golwende terrein is topo-edafiese patroon vorming veral duidelik, omrede reën wat op golwings val graviteer vanaf die hoogste na die laagste dele via hellings waardeur opgeloste material en gronddeeltjies verplaas word. Die opeenvolging binne landskap-golwings tesame met geassosieerde grond en plantegroei staan bekend as "katenas". In die KNP word relatiewe oop plantegroei op sanderige grond op die kruine van katenas gevind, en digter plantegroei op klei gronde wat meer voedingstowwe en water bevat word in valleie aangetref.

Valleie en laagliggende gedeeltes van die katena het daarom dikwels plantegroei van hoër gehalte en hoeveelheid, bly langer groen in die droë seisoen en is dus belangrik vir herbivore gedurende dié seisoen. Voorts lewer die digter plantegroei van laagliggende gedeeltes van die katena skaduwee aan sensitiewe diere, vergeleke met die oper plantegroei op katena-kruine. Die plantegroei in die laer gedeeltes van die katena kan dus belangrik wees vir olifante wat moontlik fisiologiese probleme kan ondervind om van hitte ontslae te raak gedurende tydperke van uitermatige hoë omringende temperature. Hoofstuk 2 dui aan dat olifante op en af met die katena-gradiënt beweeg in sikliese ritmes wat die seisoenale patrone in reënval en sirkadiese patrone van sonuitstraling en temperatuur volg. In die droë seisoen en gedurende die middag verkies olifante om hoofsaaklik in die laer gedeeltes van die katena te wees, maar vertoon geen voorkeure oor die katena-gradiënt in die nat seisoen en gedurende die nag nie. Lokale topografie is daarom belangrik in savanna ekosisteme, omrede dit, in wisselwerking met klimaat, die verspreiding van voedingstowwe en vog oor die landskap beheer, plantegroei patrone en -produktiwiteit beïnvloed en die verspreiding van groot herbivore affekteer.

Daarna, in Hoofstuk 3, vra ek die vraag of, en indien wel die geval, deur welke meganismes herbivore ruimtelike patroon vorming in savanna plantegroei kan inisieer. Deur gebruik te maak van simulasie modelle het ek die aannames dat herbivoor-plantegroei terugvoering asook die konteks van die omgewing nodig is vir herbivore om ruimtelik plantegroei-patroon vorming te inisieer. Die model wys dat herbivore plantegroei-patroon vorming kan inisieer slegs as twee sleutel aannames nagekom word. Eerstens moet hulle die aantreklikheid van die gebied verbeter terwyl hul wei, sodat hulle dié gebied weer sal besoek, byvoorbeeld, deur 'n toename in weidings-beskikbaarheid of kwaliteit. Die model wys dat grasvreters in staat is om permanente wei-grasperke deur 'n positiewe terugvoer siklus (beweiding-hergroei-her beweiding) te onderhou wat verhoogde produktiwiteit in kort gras-stande skep, met plantegroei van verhoogde kwaliteit. Blaarvreters onderdruk egter die werwing van bome om volwassenheid te bereik en verhoog daardeur die gedeelte van die kroon wat binne blaarvreters se bereik is. Tweedens moet beweiding ruimtelik eksplisiet wees, byvoorbeeld, wanneer beweiding in 'n gebied die plantegroei beïnvloed by groter ruimtelike skale of wanneer die plantegroei in groter ruimtelike skale die seleksie en benutting van 'n gebied beïnvloed. Nie-teenstaande wys die model dat vooraf-bestaande ruimtelike plantegroei patrone die proses van plantegroei patroon vorming deur beweiding beïnvloed, alhoewel hierdie invloed afneem wanneer die heterogeniteit en skaal van kollerigheid ("patchiness") van die oorspronklike plantegroei afneem. Voorts vind plantegroei-patroon vorming slegs plaas by gemiddelde herbivoor digthede, want hoë herbivoor digthede lei tot die homogenisering van plantegroei.

Dus kan die positiewe plant-herbivoor wisselwerking herbivore stimuleer om gereeld vooraf-besoekte gebiede weer te besoek wat tot gebied-afhanklikheid lei. In Hoofstuk 4 het ek daarom die patrone geanaliseer van gebied-afhanklikheid in olifante in die KNP deur te bereken hoe besoeke na spesifieke gebiede in die landskap vergelyk met besoeke van gebiede in die verlede. Ek fokus spesifiek op die invloed van twee hoof hulpbronne van olifante, naamlik plantegroei en water, op die patrone van gebied her-besoeke. Omdat die beskikbaarheid van oppervlakwater seisoenaal varieer en omrede plantegroei afhanklik is van seisoenale reënval-patrone, het ek die patrone van gebied her-besoeke in verband met hierdie hulpbronne gebring deur die seisoensverandering van reënval in ag te neem. Die resultate dui aan dat olifante nie voorheen-benutte gebiede vermy nie, maar blyk om 'n neiging te toon om terug te keer na gebiede voorheen besoek teenoor wat van ewekansige bewegings verwag sou word. Die patrone van gebied-afhanklikheid was ook nie alleenlik bepaal deur die voorkeure vir sekere gebiede onafhanklik van vorige ondervindings nie, omrede sommige gebiede dikwels besoek is maar nie baie her-besoek is nie terwyl ander gebiede nie baie besoek is nie, maar gereeld her-besoek word. Die olifante was meer geneig om gebied-getrou te wees wanneer oppervlak water skaars was, m.a.w., gedurende die droë seisoen, asook in gebiede naby water. In teenstelling hiermee was dit nie die geval vir vroulike olifante betreffende gebiede naby water nie, moontlik omdat hierdie gebiede nie net water maar ook skuiling en volop weiding van hoë voedingswaarde gebied het. Alhoewel ons nie sterk, algehele verskille tussen manlik en vroulike olifante gevind het nie, het vroulike olifante blykbaar die tydstip van her-besoeke aan sekere gebiede beplan deur omgewings- en klimaatstoestande in ag te neem. Dit mag te make hê met die strenger voorwaardes betreffende die kwaliteit en beskikbaarheid van weiding vir vroulike olifante en jong individue in familie troppe. Ons hipotese is dat dít die insentief is om hergroei van vooraf-benutte plante te vreet. Breedweg wys Hoofstuk 4 daarop dat familiariteit betreffende sekere gebiede 'n groot invloed op die bewegings van olifante het.

Die volgende twee hoofstukke (Hoofstukke 5 en 6) fokus op die invloed wat die ruimtelike skaal van ontleding op die kwantifisering en voorspelling van spesie verspreiding het. Hoofstuk 5 lig die wisselwerking tussen ruimtelike outokorrelasie in die residue van regressie metodes en die ruimtelike skaal verandering van spesie-omgewing verwantskappe uit. Deur gebruik van 'n hipotetiese spesie in 'n kunsmatige landskap wys hierdie hoofstuk die gevolge van 'n ontoepaslike skaal op sulke analisering asook die interpretasie daarvan. Naamlik, Hoofstuk 5 wys dat 'n foutiewe passing van die skaal van analisering en die skaal van 'n spesie se respons op sy omgewing lei tot 'n verlaagde proporsie van die variasie wat verklaar word deur omgewings-faktore. Dit het ook residuele outokorrelasie (RSA) en verwronge regressie-koëffisiënte tot gevolg. Die grootte van die fout-voorspeller afhanklikheid hang af van die wisselwerking tussen die skaal van landskap-heterogeniteit en die skaal van 'n spesie se respons op hierdie heterogeniteit. Omrede fout-voorspeller korrelasies moeilik is om te diagnoseer, is hierdie 'n ernstige problem vir ruimtelike analisering van spesie verspreiding. In Hoofstuk 5 word egter aangetoon dat om eksplisiet skaal effekte op RSA in ag te neem, die skaal waarby 'n spesie op sy omgewing reageer kan uitwys. Dit is belangrik, want in Hoofstuk 5 word aangetoon dat die skatting van spesie-omgewing verwantskappe deur ruimtelike regressie metodes te gebruik foutief is in die geval van 'n ontoepaslike skaal, wat aanleiding gee tot vals gevolgtrekkings wanneer skaal vraagstukke nie eksplisiet in ag geneem word nie. Dus beklemtoon hierdie hoofstuk die belangrikheid om die toepaslikheid van

ruimtelike skaal wat in analises gebruik word te ondersoek, aangesien skaal foute die sterkte van statistiese analises asook die vermoë om die prosesse wat ruimtelike patroon vorming in ekologiese verskynsels te verstaan affekteer.

Daarom analiseer ek in Hoofstuk 6 die breë verspreidingspatrone van olifante in KNP en fokus op die ruimtelike skaal waarby olifante reageer op hul hoof hulpbronne, naamlik water en weiding. Hierdie hoofstuk toon aan dat die insluiting van omgewings konteks by 'n toepaslike skaal die kwantifisering van habitat seleksie verbeter en die voorspellingsvermoë van habitats-geskiktheid modelle verhoog. Die olifante reageer op hul omgewing in 'n skaal-afhanklike wyse met weidings eienskappe wat die habitat seleksie aandryf by growwe ruimtelike skale en oppervlak water by fyner ruimtelike skale. Daar is gevind dat olifante geslag-skeiding toon in habitat seleksie, hoofsaaklik as gevolg van hul respons op plantegroei en topografie. Manlike olifante verkies gebiede met hoë boom bedekking, maar vermy gebiede met hoë gras biomassa, terwyl dié patroon omgekeer is vir vroulike olifante.

In Hoofstuk 7 word die gevolgtrekkings wat gemaak kan word in die voorafgaande hoofstukke verwerk en die vraagstukke aangespreek word in die breër konteks van spesie-omgewing verwantskappe geplaas. Ter opsomming, hierdie tesis toon aan dat herbivore in staat is om gesamentlik ruimtelike patrone in plantegroei- en herbivoor verspreiding te skep, selfs in die afwesigheid van onderliggende ruimtelike heterogeniteit as gevolg van positiewe plant-herbivoor interaksies. Fisiese prosesse, wat byvoorbeeld verwant is aan klimaat en topografie, skep duidelike ruimtelike- en tyds-heterogeniteit van die hulpbronne benodig deur herbivore, asook die abiotiese toestande wat hul fisiologie beïnvloed. Die skaal van omgewings-heterogeniteit kan die skale waarby spesies op hul omgewing reageer bepaal, maar hul reaksie op omgewings variasie kan ook spesie spesifiek wees. In iedere geval, die analisering van spesie-omgewing verwantskappe by ontoepaslike skale lei hoogs waarskynlik tot wanvoorstellings in die kwantifisering en voorspelbaarheid van spesie-omgewings verwantskappe. Daarom is dit 'n aansienlike uitdaging in ekologie om toepaslike skale, wat relevant is vir die studie-organismes, te beskryf. Asook om hul reaksie tot omgewings-heterogeniteit akkuraat te meet by daardie skale. Deur eksplisiet die invloed van die ruimte-tyd skale en die konteks van die wisselwerking tussen organismes en hul omgewing in ag te neem, maak opwindend deure oop vir die uitbreiding van kennis oor die prosesse wat die verspreiding en hoeveelheid van organismes bepaal.

Affiliation of Coauthors

Willem F. (Fred) de Boer, Frank van Langevelde, Sip E. van Wieren, Ignas M.A. Heitkönig, Cornelis van der Waal, Yolanda Pretorius, Emmanuel Mwakiwa, Edward M. Kohi & Herbert H.T. Prins:
Resource Ecology Group, Wageningen University, PO box 47, 6700 AA Wageningen, the Netherlands

Andrew K. Skidmore, Nicky M. Knox & Thomas A. Groen:
Faculty of Geo-Information Science and Earth Observation, University of Twente, PO Box 6, 7500 AA Enschede, the Netherlands

Rob Slotow, Bruce R. Page & Audrey Delsink:
Amarula Elephant Research Programme, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa

Michael B. Coughenour & Gabriela Bucini:
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523-1499 USA

Steve Henley & Michelle Henley:
Applied Behavioural Ecology and Ecosystem Research Unit, School of Environmental Sciences, University of South Africa, Private Bag X5, Florida 1710, South Africa

Gerrit Gort:
Biometris, Wageningen University, P.O. Box 100, 6700 AC Wageningen, the Netherlands

Claudius A.D.M. van de Vijver:
Plant Production Systems Group, Wageningen University., PO Box 430, 6700 AK Wageningen, the Netherlands.

Rina (C.C.) Grant:
Scientific Services, Kruger National Park, Private Bag X402, Skukuza 1350, South Africa

Mike Peel:
ARC Range and Forage Institute, PO Box 7063, Nelspruit 1200, South Africa

Acknowledgements

$\mathcal{W}$ith the completion of this thesis, a wonderful phase in my education and scientific career comes to an end, namely the privilege of being a PhD candidate. I was very fortunate in getting the chance to work on a topic that fascinates me so much, as well as in getting the possibility to work and interact with so many wonderful people. In retrospect, the content of my PhD research and the process of conducting the research shared an important component: *context*.

One of the central topics of this thesis is that ecological phenomena cannot be fully understood when looking at local information only: the influence of spatial and temporal context must be considered in order to see the bigger picture. Similarly, conducting (PhD) research can only be appreciated fully if it is seen in its proper context. Doing research is not just working in isolation in a dusty room (although I guess I'm quite good in this); it requires the support of and interaction with many people. This thesis could not have been completed without the endless support of many people. Several of them are already thanked for intellectual or material support in the acknowledgements of the individual chapters or by means of co-authorship, however many more did not yet receive any credit.

First of all, I would like to express my gratitude to Herbert, Andrew, Frank and Fred for being such a great supervisory team the past years. You took care of a solid scientific basis for my development, always gave me critical (constructive!) feedback and suggestions and introduced me to different viewpoints (e.g., from a satellite's perspective high above Earth to a plant's perspective solidly rooted in the soil). Thank you for believing in me and for being patient. I was blessed to have you all in my supervisory team!

Frank, after having worked with you already from 2003, I remember our first official meeting when I was appointed as a PhD candidate. First, we were chatting as always about ecology, elephants, scale and the like, but also about moralism, cars.... Then you suddenly looked very serious, and said to me that I shouldn't work to make you happy, or the group or someone else, but to do that what makes me happy. This, in a nutshell, is how I have experienced working with you: apart from being a great supervisor for content-related issues (critical as always, and the editor of my texts - even finding missing dots or wrongly placed commas in the references), you were also of great value to me regarding supervising the process of conducting research and developing myself as a scientist. For this, I owe you many thanks! Over time, supervision from your side gradually turned into co-operation between us: I am sure this will continue in the future!

Herbert and Andrew, similar things can be said about you. Although our meetings were less frequent, I really enjoyed our interesting and inspiring conversations about ecology, science and life. I feel privileged to have been working under your wings! Fred, in your function of co-ordinator of the TEMBO programme, you were linked to my PhD

research, yet officially you were not part of my primary supervisory team. However, reality proved the contrary, and enthusiastic as ever you were always willing to be involved in my project. Thank you for this! You have been invaluable for the TEMBO project!

Also many thanks to my fellow TEMBO-PhD colleagues Cornelis, Yolanda, Emmanuel, Edward and Nicky! I really enjoyed being in a team with you. Not only did I benefit a lot from your expertise regarding elephants and the African bush (I have been there a couple of times, but that does not come close to the experience that you have!), it was also good to walk the PhD route together! Cornelis and Yolanda: thank you for your hospitality at your camp in Umbabat! Yolanda and Emmanuel: many thanks for your generous laughs and heart-warming smiles! Cornelis: thank you for translating my summary into Afrikaans. Edward: Asante sana! I liked sharing a room with you, and will not forget the many good talks we had! Nicky, it was always good to meet you, mostly outside Wageningen or Enschede, even running into each other in Kruger!

Furthermore, it is a pleasure to thank those from Wageningen, as well as from abroad who collaborated within the TEMBO programme, as their input was invaluable regarding data acquisition, knowledge transfer, feedback, modelling, as well as having a good time over a beer! Thank you Ignas, Sip, Rob, Bruce, Audrey, Mike (C), Gabriela, Rina, Izak, Sandra (and other SANParks personnel), Mike (P), Steve and Michelle. I feel privileged to have been in working with you, and thank you for your hospitality and warm-heartedness during my visits to South Africa and the United States.

Furthermore, I am most grateful to the administrative staff of both REG and ITC, who were always willing to help me out and support me. Thank you Esther, Gerda, Margreet, Patricia and Willemien! Geerten and Thomas, thank you for always being there for a good chat, advice or some pieces of code. Ralf and Paul, thank you for being willing to stand by my side during my defence! And thanks to all the people at REG and ITC for the pleasant atmosphere, the conversations and discussions during the coffee and lunch breaks: Andrew, Anil, Anna, Anne-marie, Arend, Audri, Bas, Benson, Christiaan, Cornelis, Daniel, Edson, Eduardo, Edward, Emmanuel, Euridice, Farshid, Frank, Fred, Geerten, Gerda, Herbert, Herman, Ignas, Ivonne, Jasja, Jasper, Kyle, Laurens, Lennart, Mariaan, Milena, Nicky, Nicol, Patrick, Pim, Priya, Ralf, Robert, Ron, Rudy, Shadrack, Sip, Sisi, Steven, Tessema, Thomas, Tiejun, Tom (H), Tom (vd H), Tsewang, Vincent, Xavier and Yolanda.

I would also like to thank the members of the PE&RC PhD Council (PPC . . . PSP . . . PCP . . . ?) and Wageningen PhD Council (WPC) for the pleasant meetings about PhD related issues, but also the good times when organizing the annual PE&RC-Days or the Wageningen PhD party, or when having a dinner together. Thank you Agniezka, Alejandra, Ane-Marie, Anna, Arnoud, Bart, Bas, Cathelijne, Christian, Claudius, Clemens, Daniela, Diana, Diego, Dirk, Eddy, Edwin, Flavia, Frans, Jeroen, Jessica, Jochem, Joeri, Jose, Lennart, Leonie, Marjolijn, Mark, Maryia, Myriam, Onno, Roland, Simone, Stefan, Tatiana, Tosca, Tullu and Van-Anh.

Finally, I want to thank my family and friends, and especially my parents, brother, sister, and family-in-law for continuous support. And Marcella: thank you very much! I have no words to thank you for your continuous friendship and everlasting support.

Thanks to all of you, for making the past years a truly memorable experience!

Curriculum Vitae

Henrik Johan (Henjo) de Knegt was born on December 20, 1980 in Apeldoorn, the Netherlands. In 1999, he obtained his high school degree at CSG Sprengeloo in Apeldoorn, after which he moved to Wageningen to start with the MSc Forest and Nature Conservation at Wageningen University.

In his first MSc thesis, supervised by Frank van Langevelde, Fred de Boer and Geerten Hengeveld from Wageningen University and Kevin Kirkman from the University of KwaZulu-Natal, South Africa, he studied the influence of patch density on the movement patterns and foraging efficiency of large herbivores. For this he conducted field work at Ukulinga Research Farm, Pietermaritzburg, South Africa. In his second MSc thesis, he worked together with Frank van Langevelde, Thomas Groen, Claudius van de Vijver and Herbert Prins to model the influence of herbivory on the spatial patterning in savanna vegetation. He spent his internship under the wings of Chris Loggers at the USDA Forest Service at the Three Rivers Ranger District of Colville National Forest, Washington, USA. Here, he participated in the manifold aspects of the management and conservation of natural resources.

After obtaining his MSc degree at Wageningen University (*cum laude*) in 2005, he stayed in Wageningen for his PhD research at the Resource Ecology Group (REG). His PhD research was part of the TEMBO (The Elephant Movements and Bio-economic Optimality) integrated program, led by REG in close collaboration with academic institutions and organizations from the Netherlands, South Africa, Australia and the United States. He was primarily supervised by Herbert Prins, Andrew Skidmore and Frank van Langevelde. His research focused on the interplay between spatial environmental heterogeneity and the movement and distribution of elephants in Kruger National Park, South Africa, and especially the roles of spatial scale and landscape context therein. His work included the analysis of large datasets as well as theoretical modelling of ecological systems.

Furthermore, he held positions in the PhD Council of the C.T. de Wit Graduate School for Production Ecology & Resource Conservation (PE&RC) since 2006, as well as the Wageningen PhD Council (WPC). Among other things, he co-organized a one-day symposium for PE&RC each year, and was member of the organising committee of the 2nd Wageningen PhD Party in 2008.

Presently, he is appointed as post-doctoral researcher at REG, focussing on the influence of spatial heterogeneity and scale on the bio-economic optimization of the management of natural resources. This project extends the work that has been done in the TEMBO programme, and includes close collaboration with scientists from IMARES (Institute for Marine Resources & Ecosystem Studies) to study the bio-economic optimization of fisheries.

List of publications

In international journals:

De Boer, WF, MJP Vis, **HJ de Knegt**, C Rowles, EM Kohi, F van Langevelde, M Peel, Y Pretorius, AK Skidmore, R Slotow, SE van Wieren & HHT Prins. Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy*, In press.

De Knegt, HJ, F van Langevelde, MB Coughenour, AK Skidmore, WF de Boer, IMA Heitkönig, NM Knox, R Slotow, C van der Waal & HHT Prins (2010). Spatial autocorrelation and the scaling of species-environment relationships. *Ecology*, In press.

Kohi, EM, WF de Boer, M Slot, SE van Wieren, JG Ferwerda, CC Grant, IMA Heitkönig, **HJ de Knegt**, N Knox, F van Langevelde, M Peel, R Slotow, C van der Waal & HHT Prins (2010). Effects of simulated browsing on growth and leaf chemical properties in Colophospermum mopane saplings. *African Journal of Ecology* 48 (1): 190-196.

Hengeveld, GM, F Van Langevelde, TA Groen & **HJ de Knegt** (2009). Optimal foraging for multiple resources in several food species. *The American Naturalist* 174 (1): 102-110.

Van der Waal, C, H De Kroon, WF de Boer, IMA Heitkonig, AK Skidmore, **HJ de Knegt**, F Van Langevelde, SE van Wieren, RC Grant, BR Page, R Slotow, EM Kohi, E Mwakiwa & HHT Prins (2009). Water and nutrients alter herbaceous competition on tree seedlings in a semi-arid savanna. *Journal of Ecology* 97 (3): 430-439.

De Knegt, HJ, TA Groen, CADM van de Vijver, HHT Prins & F van Langevelde (2008). Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos* 117 (4): 543-554.

De Knegt, HJ, GM Hengeveld, F van Langevelde, WF de Boer & KP Kirkman (2007). Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology* 18 (6): 1065-1072.

Submitted and in preparation:

De Knegt, HJ, F van Langevelde, AK Skidmore, A Delsink, R Slotow, S Henley, G Bucini, WF de Boer, MB Coughenour, CC Grant, IMA Heitkönig, M Henley, NM Knox, EM Kohi, E Mwakiwa, BR Page, M Peel, Y Pretorius, SE van Wieren & HHT Prins. The spatial scaling of habitat selection by African elephants. *Submitted*.

De Knegt, HJ, F van Langevelde, AK Shrestha, R Slotow, S Henley, AK Skidmore, A Delsink, WF de Boer, CC Grant, NM Knox, EM Kohi, BR Page, M Peel, C van der Waal, SE van Wieren & HHT Prins. The seasonal and circadian rhythms of terrain-use by African elephants. *Submitted*.

De Knegt, HJ, Y Pretorius, F van Langevelde, WF de Boer, G Gort, AK Skidmore, R Slotow, S Henley, A Delsink, CC Grant & HHT Prins. Visited sites revisited - site fidelity in African elephants. *In preparation*.

Kos, M, AJ Hoetmer, Y Pretorius, WF de Boer, **HJ de Knegt**, CC Grant, E Kohi, B Page, M Peel, R Slotow, C van der Waal, F van Langevelde, SE van Wieren & HHT Prins. Seasonal diet switch in elephant and impala in a mopane woodland. *Submitted*.

Van der Waal, C, A Kool, SS Meijer, H de Kroon, E Kohi, IMA Heitkönig, WF de Boer, F van Langevelde, RC Grant, MJS Peel, R Slotow, AK Skidmore, **HJ de Knegt**, E Mwakiwa, Y Pretorius, SE van Wieren & HHT Prins. Large herbivores alter vegetation structure through soil nutrient mediation in a semi-arid savanna: Lessons from a natural experiment with abandoned kraals. *In preparation*.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (=22 weeks of activities).

The C.T. De Wit Graduate School PE&RC

PRODUCTION ECOLOGY

& RESOURCE CONSERVATION

Review of Literature (5.6 ECTS)

- From resource selection to landscape-use: the distribution of large mammalian herbivore (2006)

Laboratory Training and Working Visits (4.3 ECTS)

- SAVANNA model training; Natural Resource Ecology Laboratory, Colorado State University, USA (2006)

Post-Graduate Courses (7 ECTS)

- Spatial temporal aspects in resource ecology; PE&RC (2005)
- Consumer-resource interactions; PE&RC / SENSE / FE (2006)
- The use of geo-information and remote sensing for the study of competing claims on land; PE&RC / ITC (2007)
- Spatial econometrics: theory and practice; PE&RC / MGS (2008)

Competence Strengthening / Skills Courses (4 ECTS)

- The art of modelling; PE&RC / SENSE (2006)
- Scientific writing; CENTA (2008)
- Survival analysis; PE&RC (2009)

Discussion Groups / Local Seminars and Other Scientific Meetings (7.6 ECTS)

- Forest and Conservation Ecology (2006)
- Mathematics, statistics and modelling (2006-2008)
- PE&RC Theme day on scale (2007)
- PhD Day on Tropical Ecology (2009)
- Spatial methods (2009)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (2.1 ECTS)

- PE&RC Introduction weekend (2006)
- PE&RC Day (2006-2008)

International Symposia, Workshops and Conferences (5.6 ECTS)

- 12th Benelux Congress of Zoology (2005)
- Annual Meeting of the Netherlands Ecological Research Network (2008 & 2009)
- 6th KNP Science Network Meeting (2008)

Courses in Which the PhD Candidate Has Worked as a Teacher (40 days)

- Animal Ecology; ESG / REG (2006-2009)