

# Mammal Community Structure in a World of Gradients

Effects of Resource Availability and Disturbance across  
Scales and Biomes

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Cover: Blue wildebeest (*Connochaetes taurinus*) by Mpaathutlwa pan, southern Kalahari, Botswana (photo: Märtha Wallgren)

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# Mammal Community Structure in a World of Gradients. Effects of Resource Availability and Disturbance across Scales and Biomes

## Abstract

Functional types are becoming central when searching for generalities in community ecology. They may help in identifying the driving factors that shape communities, as well as in formulating ecological rules. In this thesis I show that functional types of mammal species may determine the species' responses to various environmental gradients, such as of resource availability and disturbance. My data originate from two contrasting regions of the world, the arid savannas of southern and eastern Africa and the boreal forest of central Sweden, and comprise different spatial and temporal scales. Methods include distance sampling technique, wildlife triangle census, small mammal trapping, vegetation survey and GIS-analysis.

Mammal community species richness is lower in the boreal forest than on the savanna. The boreal forest ecosystem is also characterized by few species of herbivores, while the number of predators is high. In the savanna the herbivores dominate. In comparison with savannas the boreal forest is a low productive, homogeneous habitat with a high dominance of two tree species and may thus support merely a low diversity of herbivores. However, the predator diversity seems little affected by prey species diversity and is probably more so by biomass of prey.

I found indications that the Jarman-Bell principle, formulated for savanna ungulates, also applies to herbivores in the northern boreal forest. It states that due to metabolic constraints, small-sized herbivores, especially foregut fermenters, will dominate in nutrient-rich areas and large-sized herbivores, especially hindgut fermenters, in nutrient poor areas. The results show that under high-nutrient conditions most boreal herbivores belong to the smaller of two mass classes, while there was no pattern under low-nutrient conditions. The smaller herbivores, as well as the foregut fermenters, also contributed to a larger proportion of the metabolic biomass in the nutrient-rich, compared with the nutrient-poor, area.

In summary, my results suggest similarities as well as differences between the structuring factors and processes of mammal communities depending on spatial scale and biome. I recommend that future research in community ecology center around multi-species approaches, including multiple functional types, also for questions which are traditionally restricted to few-species relationships.

*Keywords:* boreal forest, carnivores, community ecology, functional type, herbivores, Jarman-Bell principle, mammal, savanna, ungulate, wildlife.

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## Till Elsa

*Det är skönare lyss till en sträng som brast, än att aldrig spänna en båge.*

Verner von Heidenstam

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## Appendix

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Wallgren, M., Skarpe, C., Bergström, R., Danell, K., Granlund, L. & Bergström, A. Mammal community structure in relation to disturbance and resource gradients in southern Africa. *African Journal of Ecology* (In Press, Published electronically).
- II Wallgren, M., Skarpe, C., Bergström, R., Danell, K., Bergström, A., Jakobsson, T., Carlsson, K. & Strand, T. Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. (Submitted revision).
- III Wallgren, M., Bergström, R., Danell, K. & Skarpe, C. Wildlife community patterns in relation to environmental gradients and method of monitoring in a Swedish boreal ecosystem. (Submitted manuscript).
- IV Wallgren, M., Skarpe, C., Stokke, S., Danell, K., Bergström, R., Swenson, J., Motsumi, S. & Røskaft, E. Composition of body masses in two African ungulate communities - A test of the Jarman-Bell principle. (Manuscript).

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# Introduction

## Community ecology

An ecological community is an assemblage of species that coexist in time and space (McGill *et al.*, 2006). Focus is usually on one taxonomic group, e.g. mammals (Fisher and Wilkinson, 2005) or ungulates (Olf *et al.*, 2002), and on one particular temporal or geographical scale, defining the limits of the community. Studies may aim at describing present day communities or those from the past, e.g. the Pleistocene mammal fauna (Cannon, 2004). Local to regional spatial scales are most frequently used in community ecology research (Huston, 1999), but there is a growing interest for very large-scale studies as well, e.g. continental and global scales (Brown, 1995; Blackburn and Gaston, 2002).

The species composition of any ecological community is ultimately determined by speciation, extinction, immigration and emigration of species. These processes are strongly affected by abiotic factors, such as climate, altitude and disturbance regime, as well as biotic interactions, such as competition, predation and facilitation (Huston, 1999). The abiotic conditions, that a community experiences, may govern the intensity of different biotic interactions.

Community ecology is currently focusing more on functional than on descriptive properties. Thus, functional traits are becoming central when searching for generalities in community ecology. In short a functional trait is a measurable property that relates to the function of a species, e.g. feeding type or body size, and should vary more between than within species (McGill *et al.*, 2006). Syndromes of functional traits that are similar among several species characterize functional types, which are regular and important components in studies of community structures. Examples of functional

types are large-sized herbivores, small-sized carnivores or volant insectivorous mammals. Focusing on functional types, rather than on species, gives information on why, instead of only how, communities differ in composition. When several species respond in the same ways to abiotic or biotic variables and the responses may be related to shared functional characteristics of the animals, it gives a good foundation for identifying the driving factors that shape the communities, as well as for formulating general ecological rules. Such conclusions are often more difficult (and bold) to draw from studies of just one species.

## Mammal community ecology

### Mammal assemblages

There are profound differences between indigenous mammal communities in different parts of the world and even within biomes. Among the continents Africa has by far the highest diversity and biomass of large-sized mammals (Sinclair, 1983; du Toit, 1995). Most of them inhabit the savannas of eastern and southern Africa (Huntley, 1982). South America resembles Africa regarding e.g. latitudinal location, continental shape and occurrence of tropical savannas, but is in spite of that home to a low abundance and richness of large-sized mammals (Eisenberg, 1981). A very high proportion of endemic mammals is found in Australia, which otherwise exhibits moderate mammal species richness, only representing four taxonomic orders (Cellabos and Brown, 1994). In Europe there are significant differences in the distribution of body masses and feeding types between different biomes (Danell, 1999) and in Eurasia and North America mammal community compositions, such as species richness, vary with e.g. longitude (Danell *et al.*, 1996) and biogeographical regions (Bruzgul, 2007).

### Resources and disturbances

Mammal species richness can roughly be extrapolated from land area (Danell *et al.*, 1996) as well as biogeographical and evolutionary history of the habitat (Cannon, 2004). Moreover, both historic and present day mammal community compositions relate to ecosystem specific levels of resource richness, such as primary production (Abramsky and Rosenzweig, 1984), and disturbance, through their effects on speciation, extinction, immigration and emigration of species (Huston, 1999; review in Wallgren, 2005). The task of separating and evaluating components of resource richness and disturbance is a complex one, not least since both factors are

heterogeneously distributed and different species may respond very differently to their variability and gradients (Paper I).

Ecosystem productivity correlates with resource abundance, heterogeneity and amount of rare resources (Wright, 1983; Abrams, 1988) and is a major determinant of mammal species diversity (Olf *et al.*, 2002). Several different components may collectively determine and regulate the productivity of an ecosystem. Most studied are the effects of temperature, rainfall and soil nutrients on primary production, i.e. food availability for mammalian herbivores (Bell, 1982; Illius and O'Connor, 2000; Olf *et al.*, 2002). Coe *et al.* (1976) showed that biomass of African ungulate communities is positively correlated with annual rainfall up to ca. 700 mm per year and Bell (1982) emphasized the importance of soil nutrients in addition to moisture. Likewise, species diversities of mammals in Europe and North America often correlate with components of productivity, such as temperature (Danell *et al.*, 1996) and elevation (Badgley and Fox, 2000).

Disturbances are common and naturally occurring features of most ecosystems in the world (Nelleman *et al.*, 2001). Large-scale disturbances include e.g. earth quakes, droughts and glaciations and may have profound effects on the mammal faunas in different regions. Also local mammal abundances and species compositions may vary conspicuously with spatial and temporal heterogeneity of natural and human induced disturbance, e.g. altered fire regimes, hunting by humans, habitat change and habitat loss (Brashares *et al.*, 2001; Fritz *et al.*, 2003). Increases in human populations are often connected with loss of wildlife key resources (Fritz *et al.*, 2003; Paper I). A general rule is that there is a positive relationship between spatial and temporal scales of events, such as disturbances (Niemelä, 1999). More importantly, the effects of the disturbances on communities are also scale dependent, but not always straightforwardly so. Barriers in the landscapes, e.g. fences or roads, may be local phenomena, but affect mammal communities over a whole region, especially in ecosystems where some species are migratory.

### Species interactions

Many biotic factors contribute to the shaping of mammal communities, e.g. predation, facilitation and competition, and complicate the assemblage rules of the communities. These factors are often described as general principles and can be applicable on widely different communities, often world wide.

Predation can be a major driving factor of, alternatively appear totally detached from, prey population dynamics (Vucetich and Peterson, 2003; Grange and Duncan, 2006). Top-down (i.e. predator controlled) and

bottom-up (i.e. food resource controlled) processes have been studied and debated over for innumerable few-species assemblages, e.g. the classical example of moose (*Alces alces*) and wolf (*Canis lupus*) on Isle Royale, North America (Vucetich and Peterson, 2003), or ungulates and large carnivores in Africa (Grange and Duncan, 2006). Either process is bound to be dynamic, because primary production is not a constant input (see above) and both prey and predator populations are exposed to the forces from other abiotic and biotic variables.

Although body size of the most common prey usually links to the size of the predator (Carbone *et al.*, 1999), carnivores may exploit a wide range of prey, often at least one order of magnitude over as well as under its own size (Owen-Smith and Mills, 2008). In practice this means that small-sized carnivores may kill small- to medium-sized prey, while large-sized carnivores may kill prey of all size classes (Sinclair *et al.*, 2003).

While mammalian carnivores are food generalists as well as opportunists, most herbivores are highly selective both in space and time. This is an inevitable effect from vegetation being a strongly heterogenous food resource. It may vary significantly in quantity and quality (i.e. protein and carbohydrate contents combined with digestibility) depending primarily on moisture and soil nutrients (Bell, 1982). Prey for carnivores have a more constant nutritive quality. In the same time the energy demands of herbivores are not linearly related to body size. Instead, small-sized animals have higher metabolism in relation to body mass compared to large-sized animals (Hofmann, 1973). Therefore the largest herbivores can tolerate a lower quality of food than smaller herbivores, as long as the low-quality food is abundant (Demment and Van Soest, 1985).

Herbivorous species can be arranged along a continuum of grazers, intermediate mixed feeders (sometimes separated between those that are preferably grazers and those that are preferably browsers) and browsers depending on major food choice (McNaughton and Georgiadis, 1986). Grazers are generally large-sized bulk (high quantity) feeders and browsers small-sized selective (high quality) feeders (McNaughton and Georgiadis, 1986; Olf *et al.*, 2002), but exceptions include e.g. moose, which is the largest herbivore of the boreal zone, as well as a browser. Other exceptions are giraffe (*Giraffa camelopardalis*) and black rhinoceros (*Diceros bicornis*), both large-sized browsers on the African savannas.

Mammalian herbivores can profoundly influence properties of their own food resources, e.g. nutrient cycling, net primary production and fire regimes (Hobbs, 1996). Modification of vegetation by large-sized species

may facilitate small-sized species, both within grazer (Frank *et al.*, 1998) and browser guilds (Skarpe *et al.*, 2000; Makhabu *et al.*, 2006).

The nature and consequences of competition have been thoroughly studied in mammal ecology. Competitive relationships may occur between carnivores, e.g. large-sized carnivores depleting prey resources for smaller ones (Owen-Smith and Mills, 2008), as well as between herbivores, e.g. by changing or monopolizing grazing or browsing resources (Murray and Illius, 2000; Arsenault and Owen-Smith, 2002). There is also evidence of resource partitioning (Makhabu, 2005), a possible outcome of coevolution, perhaps masking competitive relationships in the past.

Even though most studies of biotic interactions involve merely few-species assemblages (instead of all potentially interacting species) their outcomes are often ambiguous, perhaps complicated by e.g. combined effects of predation, facilitation and competition (Sinclair, 1985), as well as the great variety of abiotic factors.

## Mammal communities in focus

The present study focuses primarily on terrestrial, non-volant mammals with body masses from a few grams up to several tons. Wild and domestic species of all feeding types have been included. In addition, a few selected wild bird species, e.g. ostrich (*Struthio camelus*) and capercaillie (*Tetrao urogallus*), are included on the basis that they functionally resemble or interact with the mammals.

Several spatial and temporal scales are covered under the different objectives of the study. Spatial organizations comprise local, landscape, regional and global scales and temporal scales are daily, seasonal and quarter of a century. My data originate from two contrasting regions of the world: the arid savannas of southern and eastern Africa and the boreal forest of central Sweden. These widely different data sets give me a unique possibility to compare properties, define determinants and ultimately understand the function of mammal communities across the borders of biomes. This is an important step in mammal community ecology research and from many aspects a step yet to be taken.

Few studies have focused on large-scale patterns in the composition of mammalian multi-species assemblages and especially on those which encompass several different functional types, e.g. feeding types or size classes. Nevertheless, studies of this kind may provide important information on the nature of mammal communities and more importantly the driving factors behind their composition. Ultimately the results of such

studies may be used for formulating general rules regarding mammal community ecology and dynamics and in the long run guide decisions concerning management and conservation of natural mammal communities.

## Objectives

The aim of my thesis was to study how mammal community composition of species and functional types vary along environmental gradients, mainly derived from measured components of resource availability and disturbance, on multiple spatial and temporal scales. The ultimate aim was to find general regularities in, or differences between, communities due to some intrinsic, geographically independent, responses of mammal assemblages to abiotic and biotic conditions. More specifically the aim was covered as follows in papers I-IV:

(I) How does mammal community composition of species and functional traits vary along gradients of disturbance and resource availability in the African savanna?

(II) How do various kinds of human land use affect mammal species richness and abundances in the African savanna?

(III) How do patterns in wildlife community composition relate to environmental variation on landscape scale in the boreal forest?

(IV) What is the composition of body masses in two African ungulate communities? A test of the Jarman-Bell principle.

## Study areas

The study areas are situated in two African savanna ecosystems, the Kalahari, Botswana, and Serengeti, Tanzania, and in one forest ecosystem in the boreal zone of central Sweden, more specifically encompassing the counties of Värmland and Örebro. The areas are fairly large-sized (from ca. 10 000 to 40 000 km<sup>2</sup>), corresponding to landscape scale, and include heterogeneously distributed resources and disturbance regimes.

### Africa

#### South-western Kalahari

The south-western part of the Kalahari is a semi-arid savanna. It is characterized by low and variable rain fall, averaging about 250-350 mm/year (Botswana Department of Meteorological Services, BDMS, unpubl. data). Precipitation occurs during the summer months November-April. The landscape is covered by dry bush savanna on nutrient deficient sand and lacks natural permanent water sources. A key geomorphic feature of the Kalahari is the pans, shallow depressions, with clayey, water-impenetrable bottoms (Lancaster, 1974). They collect rain water and may contain mineral licks and more nutrient rich vegetation than the surrounding savanna. Pans are key resources for many wild mammal species (Bergström and Skarpe, 1999; Paper I).

Centrally located in the approximately 40 000 km<sup>2</sup> study area is a group of livestock-keeping villages. Surrounding the villages are communally managed rangelands holding livestock, primarily cattle, which forage unattended up to 20-25 km from the villages (Bergström and Skarpe, 1999; Paper I). Within these communal grazing areas fenced livestock ranches have been established. Starting at 40-80 km from the villages are wildlife

management areas and in the south, about 80 km from the villages, a national park, the Kalahari Transfrontier Park. Water for humans and livestock is supplied mainly from bore-holes within communal grazing areas, ranches and close to settlements within wildlife management areas.

Wildlife used to be abundant in south-western Kalahari (Child and Le Riche, 1969), but has decreased dramatically since the end of the 1970's (Crowe, 1994; Paper I). Competition with livestock, droughts, erection of cordon fences across migration routes and hunting are possible causes of the declines. One conspicuous event in the Kalahari was the major die-off of wildebeest (*Connochaetes taurinus*) around 1982-83. An estimated 90% of the population died when their drought-induced migration was hindered by fences (Spinage, 1992).

#### Northern Kalahari, Chobe National Park

Chobe National Park of over 10 000 km<sup>2</sup> is located in northern Botswana. Rainfalls occur mainly between November and April and the yearly precipitation is 450-600 mm (BDMS, unpubl. data). The study area comprises mainly arid savanna woodlands on nutrient-deficient Kalahari sand, but also alluvial shrublands and diminishing riparian forests close to the Chobe and Savuti riverbeds (the former has permanent water, while the latter is dry) and Savuti marsh (Cooper, 1990; Skarpe *et al.*, 2004). Chobe is known for dense and species rich wildlife populations, including e.g. some of the highest densities of African elephant in the world (Vandewalle, 2003).

#### Serengeti National Park

The Serengeti-Mara ecosystem of some 27 000 km<sup>2</sup> is located in Tanzania and Kenya. Our study was situated in Tanzania, mainly within Serengeti National Park (14 750 km<sup>2</sup>), but also crossing into some adjacent conservation and open (unprotected) areas. Precipitation occurs mainly during March-May and November-December and amounts to between ca 500 and 1 000 mm per year, with a strong gradient of increasing rainfall towards the north (Sinclair and Arcese, 1995). The volcanic soil is of recent origin and relatively high in nutrients (unpublished references cited in Bell, 1982). Vegetation types include mainly grassed plains and *Acacia* woodlands (Sinclair and Arcese, 1995). Serengeti is known for massive migrations of grazing ungulates including blue wildebeest, plains zebra (*Equus quagga*) and Thomson's gazelle (*Gazella thomsoni*) (e.g. Bell, 1971; Frank *et al.*, 1998).

## Sweden

### Värmland and Örebro counties

The boreal study area covered the Mid-Swedish counties of Värmland and Örebro, an approximate area of 26 000 km<sup>2</sup>. Average precipitation is 600–900 mm/year with the higher amounts in the west and southwest (Swedish Meteorological and Hydrological Institute, SMHI, unpublished data). The number of days with snow ranges from ca. 75/year in the south to ca. 200/year in the north (SMHI, unpublished data).

The area is dominated by boreal forest in the north and agricultural land in the south-southeast. The boreal zones encompassed are (from north to south) the northern boreal, middle boreal, southern boreal and hemiboreal zones (Ahti *et al.*, 1968). The variation in climate, latitude vegetation and land use within the study area is thus fairly large with a strong gradient from north (or northwest) to south (or southeast). Also, numerous lakes, rivers and mires occur forming a variable landscape, compared with many other similar-sized areas within the boreal forest zone.

# Methods

## Field methods

### Distance sampling

In Kalahari and Serengeti abundances of medium and large-sized mammals (> approx. 0.2 kg) were estimated mainly by transect counts using the Distance sampling technique (Buckland *et al.*, 2001). Two observers standing on the back of a 4x4 vehicle spotted animals along sandy tracks circuiting the study areas, in night-time using spotlights. Species and group size were determined and the perpendicular distance between the animal(s) and the track was calculated from measurements of distance and angle taken with a range-finder (Buckland *et al.*, 2001). Using pre-existing tracks is not optimal, since they are not randomly positioned in the landscape, but the thorny vegetation and heavy sand precluded the use of randomly placed transects. Nomenclature for mammals follows Skinner and Chimimba (2005) for Kalahari, Estes (1992) and Sinclair and Arcese (1995) for Serengeti.

### Wildlife triangle census

In Sweden relative abundances of animals were estimated from track counts along a total of 222 equilateral triangular routes, each with 12 km perimeters. The triangles were systematically positioned in Värmland and Örebro counties, Sweden. The triangles encompassed different latitudes and altitudes and included varying proportions of e.g. forested and agricultural areas, heterogeneity, infrastructure and water. Forest types and succession stages also differed between triangles. Inventories were performed according to the technique developed in Finland (e.g. Lindén *et al.*, 1996). Track

inventories were made January–March of 2001–2003, between 24 and 72 hours after a snowfall and always in one day. Each side of the triangles was searched for tracks of mammals from the size of weasel (*Mustela nivalis*) and larger, as well as visual observations of large-sized forest birds. Counting tracks along lines does not yield absolute measures of animal densities. Instead an index is obtained, which indicates relative differences between triangles or groups of triangles.

Pellets of 10 selected species of mammals and large forest birds were counted in 211 triangles during March–June of 2001–2003. Plots for pellet counts were placed at every 100 m along the triangle sides. Only pellets dropped after leaf fall, estimated to October 15, were included, thus giving a measurement index of relative abundance of animals during the previous winter. The track indices and pellet frequencies were related to various environmental variables (extracted from GIS maps, details below).

#### Additional field methods

The small mammal (<0.2 kg) community of south-western Kalahari was sampled at 13 sites during the dry season of 2002. At each site twenty-four collapsible and ventilated Sherman's live traps were laid out along a transect starting at the edge of a pan and stretching 5 km into the adjacent savanna. The traps were baited and checked a minimum of once a day for three consecutive days. Trapped animals were identified to species and marked in order to avoid resampling.

During the wet season study of 2004 a vegetation survey was performed simultaneously with the mammal counts in south-western Kalahari. At given distances along the transects some key characteristics of vegetation structure, relating to cover of grass and bush, were recorded, as well as signs of recent burns. We used circular plots with a radius of 100 m with the vehicle in the centre and the track intersecting the plot.

#### GIS data

The wildlife triangles, each one surrounded by a 1 km wide buffer, were imported into ArcMap 9.1 (ESRI Corporation, Redlands, CA). Environmental properties were assigned to the triangles using GIS maps, including the Road map (Swedish "Vägkartan"), Swedish land cover data ("Svenskt marktäckedata") and, for Värmland only, the Vegetation map ("Vegetationskartan"). All maps are distributed by National Land Survey of Sweden ("Lantmäteriet").

More specifically, each triangle with buffer was attributed by absolute area of various kinds of land cover (including forested land, wetland, arable land/pasture, lake etc.), total length of water courses and infrastructure, i.e. roads and railways, degree of heterogeneity (i.e. the summed perimeter of all features) and mean altitude. Latitude and detailed vegetation data, including the area of different forest types, compositions and stages, were also used as environmental variables.

## Statistical methods

### Multivariate analysis

Data sets that include numerous species and environmental variables are multi-dimensional by nature and highly suitable for multivariate statistics. Canoco for Windows 4.5 (Ter Braak and Šmilauer, 1998) offers a range of multivariate techniques for analyzing multi-dimensional data. We chose Principal Component Analysis, which is based on a model of linear species responses (as different from the unimodal response in Correspondence Analysis) to underlying environmental variables and arranges species or sites along axes that represent theoretical gradients. The choice was based on the linear nature of the most important environmental variables within the study areas (disturbance by humans, see details in Paper I, and altitude, latitude and amounts of agricultural area and coniferous forest, see details in Paper III). The measured environmental variables were fitted afterwards and do not affect the arrangement of the species or sites in the ordination. This step will reveal if there are important environmental variables that are not covered by the study (i.e. when part of the species arrangement does not correlate with any of the measured variables).

### Distance sampling

The data of mammal species  $>0.2$  kg comprising at least 30 observations were analyzed with Distance 3.5 Software Package (Thomas *et al.*, 1998). Distance sampling provides density estimates of animal populations even when only a proportion of the animals are detected, the animals occur in groups and the size of the sample area is unknown (Buckland *et al.*, 2001). Densities of species comprising a minimum of 30 observations were estimated using 95% confidence intervals. Central to distance sampling is the species specific detection function  $g(y)$ =(the probability of detecting an animal at a distance  $y$  from the transect). All animals on the transect must be detected, i.e.  $g(0)=1$ . Uniform, half-normal, hazard-rate and negative

exponential key functions were fitted to the observed distances and their fit evaluated based on the Akaike's Information Criteria as well as visual inspection. Data were truncated in order to improve the fit and the density estimates are based on these selected and fitted key functions. Stratification was applied based on season or land use.

# Results and discussion

## Short summary of papers

(I) How does mammal community composition of species and functional traits vary along gradients of disturbance and resource availability in the African savanna?

The study was conducted on landscape-scale in semi-arid south-western Kalahari, Botswana. We predicted that livestock-keeping villages are disturbances and pans resources for wild mammals, that the responses of the animals to the disturbance and resource gradients depend on their functional types and that increased disturbance over time has reduced the numbers and distributions of large wild herbivores.

The disturbance gradient was more important than the resource gradient for explaining the distribution of wild and domestic mammals  $>0.2$  kg. About 70% of all livestock recorded was found  $<25$  km from the villages and almost 90% of the wildlife  $>40$  km from the villages. Large and medium-sized mammals ( $>0.2$  kg) were highly affected by disturbance, herbivores more clearly so than carnivores (Paper I, Figure 1a and Table 2). The mammal communities with the highest species diversities were characterized by low total biomass and low levels of disturbance (Paper I, Figure 1b and Table 3). Small mammals ( $<0.2$  kg) were most dependent on local-scale variation in resources, probably shelter and food (Paper I, Table 5). We suggest that livestock may competitively exclude large- and medium-sized, but generally not small, wild herbivores. There may also be a potential effect from hunting by humans.

Increased disturbance over time has led to decreasing ranges and abundances of large wild herbivores (Paper I, Table 6). However, the

smallest antelope, steenbok (*Raphicerus campestris*), which is a browser, has increased in overall abundance as well as distribution close to the villages. It probably benefits from increased cover of encroaching bushes, a possible effect from heavy grazing by livestock, or from reduced wild carnivore populations close to the villages. We conclude that disturbance may disrupt the organization of functional types and consequently also the function of indigenous mammal communities in African savannas.

(II) How do various kinds of human land use affect mammal species richness and abundances in the African savanna?

Different types of human land use, e.g. pastoralism and wildlife protection, may be key determinants of wildlife populations. In this study of the wild and domestic mammal communities in south-western Kalahari, Botswana, we found that most large-sized wildlife species avoided pastoral areas (Paper II, Appendix 1). Especially the red-listed species (IUCN, 2004), including the largest antelopes and carnivores, were restricted to protection areas. Antelopes are probably affected by competition from livestock, both directly over food and indirectly through habitat modification. Wild carnivores potentially suffer from illegal hunting outside protection areas. Some medium-sized wildlife species, e.g. ground squirrel (*Xerus inauris*) and yellow mongoose (*Cynictis penicillata*) occurred in highest densities within pastoral areas and probably benefit from compact soil or increased amounts of invertebrate prey associated with livestock.

The total metabolic biomass of mammals was one order of magnitude higher in livestock areas compared with wildlife areas (Paper II, Table 3). Differences in species richness and diversity between types of land use were more pronounced during the dry season, when resources are most limited, than during wet season (Paper II, Figures 2a-b and 3b). Also, we found numerous cattle moving into wildlife areas during the wet season, probably an effect of a temporal increase in water availability.

Differences in vegetation structure depending on land use included sparser field layer vegetation and higher cover of an invasive shrub in livestock areas (Paper II, Figure 5) and are most likely caused by heavy grazing, mainly by cattle. The trapping frequency of small mammals (<0.2 kg) was highest in the national park (Paper II, Table 4 and Figure 4), where the cover and height of grass, and thus also the shelter from predators, is high. We emphasize: 1) the importance of protection areas for preserving wildlife, not least endangered species, and 2) a multi-species approach for correctly assessing the effects of human impact, such as pastoralism, on wildlife communities.

(III) How do patterns in wildlife community composition relate to environmental variation on landscape scale in the boreal forest?

The aims of this study were to investigate how the distributions of wild mammals and large-sized forest birds in the Swedish boreal forest are affected by environmental variables on landscape scale and whether there is a correlation between two monitoring techniques, pellet count and wildlife triangle census. Two herbivorous mammals, the small-sized hare (*Lepus* spp.) and the medium-sized roe deer (*Capreolus capreolus*), preferred agricultural areas, while the largest herbivore, moose, and the largest forest bird, capercaillie (*Tetrao urogallus*) showed preferences for coniferous forest (Paper III, Figures 3 and 4a-b). Overall, forest grouse seemed slightly more dependent on coniferous forest coverage than mammals (Paper III, Figures 5 and 4a-b), which may indicate that the former are more sensitive to forest fragmentation than the latter. We also found effects from forest type and stage, infrastructure and type of monitoring on the composition and distribution of the wildlife community (Paper III, Tables 1 and 2). However, we believe that our choice of landscape scale could mask additional local patterns, e.g. effects of clear-cut areas on species distributions.

The pellet count and wildlife triangles sampling techniques measured distributions over the whole winter and momentary late winter distributions, respectively, and thus reflected different choices that the animals make. A negative effect from infrastructure on the community was clear only with respect to all winter distributions, which could mean that wildlife normally avoid areas close to roads and railways, but use them temporally in late winter, perhaps for moving.

We conclude that most wildlife species of the boreal forest are habitat generalists and that important driving factors of the community composition are: 1) climate harshness and resource availability, e.g. deciduous browse, in the north, and 2) preference or avoidance of open landscape, i.e. arable land and pastures, in the south.

(IV) What is the composition of body masses in two African ungulate communities? A test of the Jarman-Bell principle.

We present regional scale empirical support for the Jarman-Bell principle, stating that due to metabolic constraints ungulate communities in nutrient-poor savannas will be dominated by large-sized species with wide food tolerances, while communities in nutrient-rich savannas will be dominated by small-sized, selective species. Focus was on the large wild herbivore communities in two African ecosystems, Chobe in Botswana and Serengeti

in Tanzania, both with similar rainfall, but with nutrient poor and nutrient rich soils, respectively.

Among four body mass classes (<25, 25-90, 90-370 and >370 kg) ungulates >370 kg had the highest density in Chobe and the lowest in Serengeti (Paper IV, Table 2). In Serengeti ungulates weighing 90-370 kg dominated. It is suggested that the herbivores of the smallest size classes are limited by something else than food resources, possibly predation. There was also a detectable difference in the metabolic biomass of high quantity feeding hindgut fermenters and high quality feeding foregut fermenters between the study areas. The former dominated in nutrient poor Chobe and the latter in nutrient rich Serengeti. On a smaller scale within Chobe we found that the small sized impala (*Aepyceros melampus*) was virtually confined to patches with richer habitat on alluvial soils.

Our results show that the biomass of the largest ungulates is not regulated solely by rainfall, but also by nutrient availability. Further, since ungulates with different body masses, feeding types and digestive systems are limited by different factors, a better understanding of the function of herbivore communities within their natural ecosystems, as well as their susceptibility to environmental change, should be achieved from large-scale studies of multi-species assemblages, ultimately from different regions of the world.

## Global scale patterns in mammal community composition

### Are boreal forest and savanna mammal communities functionally different?

Components of wild mammal community composition in the boreal forest ecosystem and the northern Kalahari ecosystem are summarized in Table 1. The areas are characterized by similar rainfall, 600-900 mm/year in the former and 450-600 mm/year in the latter (although evapotranspirative demands are very different), as well as inclusion of both productive and infertile soils. Only mammal species observed within the two study areas (species lists corresponding to Papers III and IV) are covered and thus not the smallest mammal taxa, including most rodents (e.g. Muridae), shrews (Soricidae) and elephant-shrews (Macroscelididae). Since the data sets have been collected using different methods and sampling effort, I avoid comparisons of relative observation frequencies and concentrate instead on only the structural differences in community compositions. However, it is worth noting that the boreal forest community is derived from ca. 60 000 observations (of animal tracks) and the savanna community from ca. 1 000 observations (road-side counts). The community characteristics of interest

Table 1. *Structural composition of mammal communities in two study areas, one boreal forest and one savanna ecosystem. The figures refer to number of taxonomic groups (species, families and orders) and to number of species within functional groups relating to feeding type, body mass and social structure.*

Structuring factor	Functional type	Boreal forest	Savanna
Species richness		19	55
No. of families		9	20
No. of orders		4	8
Feeding types			
	Grazer	1	13
	Browser	1	5
	Mixed herbivore	4	2
	Granivore	1	2
	Frugivore		2
	Sap- and gumivore		1
	Carnivore	9	13
	Insectivore		13
	Omnivore	3	4
Body mass (kg)			
	0.07-0.8	3	7
	0.8-6	3	14
	6-180	12	24
	180-500	1	6
	>500		4
Social structure			
	Solitary or in pairs	14	28
	Gregarious	5	27

are species richness and composition of functional types. Body mass classes have been constructed so that the body masses of all recorded species in one class are >40% larger than those in the previous class (i.e. divisions between classes occurred when the gaps in the body mass distribution is >40%). To avoid one species classes exceptions to the rule included some extremely small and large species in the low and high ends of the distribution.

Species richness is 19 in the boreal forest and 55 in the savanna mammal communities (Table 1). The boreal forest community is represented by 4 orders and 9 families of mammals, while the same figures are 8 and 20, respectively, for the savanna. The higher diversity in the savanna ecosystem may have several different explanations (e.g. Rohde, 1992), of which a thorough review is beyond the scope of this thesis. However, compared to the African savanna the boreal forest is characterized by lower productivity

and fairly short effective evolutionary time, due to e.g. several recent periods of glaciations. A consequence of low species diversity could be that competitive relationships within guilds are relaxed. However, since the Palearctic boreal forest is a homogeneous habitat, with strong dominance of only two coniferous tree species (Essen, *et al.* 1992), it is possible that the niche separation between indigenous herbivores already has reached its maximum. This does not contradict that mammals of the boreal zone are biome generalists though, since they are little affected by environmental gradients on landscape scale and since species turnover rate across the biome is rather low. Further, one must not overlook the possibility that species extinctions caused by humans also may have altered the mammal faunas of both ecosystems.

When assessing the functional structure of the mammal communities in the boreal forest versus savanna ecosystems (Table 1) the most striking difference is the dominance of carnivorous, medium-sized (6-180 kg) and solitary or monogamous mammals in the boreal forest community. In principal, half or more (up to 3/4) of the boreal forest mammal species belong to these groups, while the species are more evenly distributed among functional types in the savanna. This is important information about the function of mammal communities. Comparatively low productive, homogeneous habitats (i.e. the boreal forest ecosystem) support merely a low diversity of herbivorous mammals, the primary consumers. However, the diversity of secondary consumers, the carnivores, is little affected by prey species diversity and probably more by the biomass of prey.

The difference in distribution of body mass classes is probably mirroring the benefits of having a medium-sized body mass in the boreal forest ecosystem. The disadvantages of being too big or too small relate to limited mobility or inability to sustain high metabolic demands (Brown, *et al.* 1993), respectively, factors that probably are less significant in African savannas. Likewise, benefits of living in a group include increased vigilance and efficiency at detecting food resources (Jarman, 1974), both adaptations to life in an open landscape, such as the savanna. In closed canopy, homogeneous ecosystems the potential drawbacks of gregariousness include higher risk of being detected by predators and increased intra-specific competition.

**Does the Jarman-Bell hypothesis apply to herbivores of the boreal forest?**

A landscape scale comparison of the relative distributions of herbivore body mass classes, feeding types and digestive systems within the boreal forest is shown in Table 2. The aim is to investigate whether the Jarman-Bell

principle, formulated for savanna ungulates (Bell, 1971; Jarman, 1974), also applies to mammalian herbivore communities in the northern boreal forest ecosystem, an idea also raised in Paper IV. I use track indices from the mammal data set (see Paper III for details) as a measurement of relative abundance of animals. Unfortunately, exact figures, such as densities, can not be calculated and therefore the numbers may be biased by e.g. differences in movement patterns between species. The division between nutrient poor and nutrient rich soils is based on absolute area coniferous forest and agricultural land, respectively. Herbivore track indices of the 20 triangles with the most coniferous forest area are compared to the 20 with the most agricultural area.

Under low nutrient conditions the abundances of herbivores of two body mass classes, 0.35–35 kg and 35–350 kg (four species in each) are similar. Under high nutrient conditions most herbivores belong to the

Table 2. *Relative composition of herbivore feeding types and digestive systems within low productive (i.e. coniferous forest) and high productive (i.e. agricultural land) areas of the boreal forest biome. Numbers are given as proportions of all herbivores within each area.*

Factor	Functional group	Low productive	High productive
Abundance			
	0.35–35 kg	0.50	0.91
	35–350 kg	0.50	0.09
Contribution to metabolic biomass			
	0.35–35 kg	0.04	0.54
	35–350 kg	0.96	0.46
Abundance			
	Grazer	0	0
	Browser	0.96	0.46
	Mixed feeder	0.04	0.54
Contribution to metabolic biomass			
	Grazer	0	0
	Browser	0.49	0.10
	Mixed feeder	0.51	0.90
Abundance			
	Hindgut fermenter	0.03	0.02
	Foregut fermenter	0.97	0.98
Contribution to metabolic biomass			
	Hindgut fermenter	0.46	0.15
	Foregut fermenter	0.54	0.85

smaller class. This class contributes very little to total metabolic biomass in the low nutrient area, but to about half of the biomass in the high nutrient area. It indicates that nutrient levels in coniferous forests are not enough to support the large abundances and biomasses of small mammalian herbivores found in agricultural areas. Small herbivores have higher metabolic demands than large herbivores and thus require higher quality forage (Demment and Van Soest, 1985).

No grazers have been recorded in the selected triangles. On nutrient poor soils the abundance of herbivores is dominated by browsers, while the relative contributions of browsers and mixed feeders to the total metabolic biomass are equal. On nutrient rich soils the relationships are opposite. The abundances of browsers and mixed feeders are nearly equal, while the metabolic biomass of herbivores seems to be dominated by mixed feeders. This contradicts the expectation by the Jarman-Bell principle, that nutrient rich areas should be dominated by browsers, selecting the best parts of the high quality food (McNaughton and Georgiadis, 1986). However, the presumably scarce field layer (at least in old coniferous forests) and harsh winter climate with more snow (the amount of coniferous forest is positively correlated with increasing latitude, Figure 6a in Paper III) of coniferous forests in comparison with agricultural areas, could make coniferous forests less attractive to mixed herbivores, which partly depend on grasses and herbs for food.

The distributions of the herbivores with the two types of digestive systems indicate that foregut fermenters are more common than hindgut fermenters independent of soil nutrient levels, but that the former contribute to a larger proportion of the metabolic biomass under high nutrient conditions. The metabolic demands of herbivores are connected to digestive strategy. Foregut fermenters spend more time on processing their food than do hindgut fermenters and therefore require food of good quality, i.e. high in nutrients (Demment and Van Soest, 1985).

Consequently, the nutritional demands and foraging arrangements of mammal herbivores in the boreal forest ecosystem are, from many aspects, quite alike those of the probably most studied mammal community in the world, the large herbivores of the African savannas.

## General discussion

### Fitting mammal communities into a world of gradients

A remarkable diversity and biomass of mammals roam the southern and eastern African savannas making them suitable as well as popular for studying structures and structural processes in community ecology (Papers I, II and IV; Arsenault and Owen-Smith, 2002; du Toit, 2003; Mendoza *et al.*, 2004; Grange and Duncan, 2006). The boreal forest ecosystem on the other hand exhibits a much less diverse wildlife fauna less organized into discrete communities (Paper I). Instead, most of the animals seem to be habitat generalists. These contrasting properties are valuable for studying the effects of environmental gradients on functional structures of wildlife communities.

It is important to remember that ecological communities are not separate entities (except for in the eyes of the beholder). Generally, in the absence of barriers, such as hydrologic or topographic structures or extensive human disturbance, species compositions will change not instantly, but gradually, along environmental gradients across the globe. Therefore, I believe that the compositions of all the defined communities represent different degrees of responses to the same set of underlying environmental variables, ultimately those contributing to resource availability and to disturbance.

### Effects of resource availability and competition over resources

Ecologists have long argued that communities are non-random associations of species reflecting availability of and competition over resources (Hutchinson, 1959; Diamond, 1975; Bowers and Brown, 1982). If this is true, then the intrinsic forces that structure mammal communities anywhere on earth should be similar, or at least scaled, depending on differences in resource supplies. For example, herbivorous species of the same feeding type will compete over food if they are too similar in body size, in the same time as the possibilities of facilitation will be highest for species that are not too different in size (Prins and Olf, 1998, but contradictory results in e.g. Fritz *et al.*, 2002; Makhabu *et al.*, 2006). Similarly, carnivores of equal size class will exploit the same range of prey sizes (Carbone *et al.*, 1999). Species assemblages are therefore characterized by constant as well as optimal gaps defining classes in the continuum of functional traits, including feeding types or body sizes.

In this thesis I have shown examples of functional responses to interactions within and between functional types of mammals. In Papers I and II we argue that cattle in the savanna ecosystem outcompete only wild

herbivores of the same feeding type and size class as themselves, and that browsing herbivores of somewhat smaller body size may benefit from cattle grazing. These competitive and facilitating relationships with cattle disappear entirely in my study, when investigating distribution patterns of the smallest herbivores, those <0.2 kg (often granivorous).

We find little evidence of similar competitive relationships within the boreal forest ecosystem (Paper III). There most herbivore species over 0.35 kg are mixed feeders, while in savannas they are grazers (Table 1). Grass as a resource may support high biomasses of large mammalian herbivores (Frank *et al.*, 1998), not least through complicated processes of grazing facilitation (Bell, 1971). Nevertheless, in a highly seasonal environment, such as the boreal forest, a better strategy is probably to switch forage type (i.e. grass or browse) depending on the availability. Temperate grasslands, functionally similar to African savannas, exist in the northern hemisphere, but these are characterized by low productivity and are moderately grazed (Frank *et al.*, 1998).

We found regularities relating to community structure in high productive, i.e. resource rich, and low productive, i.e. resource poor, areas on several spatial scales (Papers I and IV). In savannas, areas rich in resources are often characterized by high diversities of both species and functional traits. In the boreal forest landscape animals seem to utilize a narrow intermediate range of resource availability (Paper III). This may further support that they are habitat generalists or indicate that much of their niche separations occur on local scale or even on patch level. Certainly, resources are not the same for different animals or in different ecosystems. Under arid and nutrient poor conditions water and soil nutrients are crucial resources for animals restricted by food, while shelter may be a resource for small animals suffering high predation pressures (Papers I and II). In a homogeneous, closed canopy forest vital resources may be scattered stands of highly palatable vegetation, attracting both primary and secondary consumers.

Current competition over resources is difficult to study, but reveals itself as contemporary or historical species exclusions. Since distribution patterns tend to be less pronounced in low productivity areas, competitive relationships are probably relaxed there and species compositions instead determined by abiotic constraints, such as temperature or length of growing season.

#### Effects of human disturbance and predation

The disturbances identified in this thesis are mostly induced by humans (although predation as well as competition within the wildlife community

also may be considered as disturbances, see below) and occur on fairly small and limited spatial scales (compared to large scale disturbance events, such as natural disasters or climatic change). Examples include pastoralism introducing new extensive competitive relationships between livestock and wild herbivores (Paper I), exclusion of animals from their natural habitats (Paper II), human infrastructure and agriculture (Paper III) and hunting (suggested effect in Paper I, and likely the reason for why e.g. black rhinoceros and white rhinoceros, *Ceratotherium simum*, are entirely missing from the species pools; Metzger *et al.*, 2007). Although spatially limited, disturbances causing disruptions of community structures may have unexpected consequences, not least since the effects of the disturbance may cascade to trophic levels above or below that of the directly affected species or guild.

The responses of wildlife to disturbances differ conspicuously, from low (Paper III) to very high (Paper II). It is somewhat surprising that the boreal forest mammal community shows weak, or inconsistent, negative response to infrastructure and little response to agricultural land (except for hare and roe deer, which were positively correlated to the latter, Paper III), while the savanna mammal species composition, on landscape scale, seems driven primarily by human land use (Papers I and II).

In dry savannas large-sized herbivore populations are regulated by rainfall (Fritz *et al.*, 2002) and soil nutrient levels (Paper IV), while small-sized herbivore populations sometimes may appear unrelated to rainfall (Grange and Duncan, 2006). The latter are instead probably regulated by predator populations (Sinclair *et al.*, 2003; Owen-Smith and Mills, 2008). Due to the feeding ecology of carnivores (i.e. being generalists and opportunists), small-sized prey species suffer a higher predation pressure than do large-sized species (see above). A reduction in predator abundance should therefore be more beneficial for small-sized than large-sized prey, since small prey is targeted by all predators. This may be why some prey species may increase in abundance as a response to human disturbance (Paper I) or why the smallest herbivorous size classes are not always the most common in nutrient rich areas (Paper IV).

In Africa mega-herbivores with a body mass over 1 000 kg are present, in many areas even abundant, and may highly affect vegetation structure, smaller-sized mammals as well as ecosystem processes including nutrient cycling (Owen-Smith, 1988; Skarpe *et al.*, 2004; Makhabu, 2005). It is evident that the mammal community of the boreal forest is missing this largest size class. It was once there composed by species like mammoth (*Mammuthus primigenius*, approximately 6-8 tons) and woolly rhinoceros (*Coelodonta antiquitatis*, approximately 2-3 tons) inhabiting a tundra-steppe

hyperzone that existed in place of extant tundra, taiga and steppe of northern Palearctic (Vereshchagin and Baryshnikov, 1991). If mega-herbivores were present in the boreal forest ecosystem, it is possible that they would have contributed to the disturbance regime and an enhanced structuring of the mammal community as well as the whole ecosystem, something that has also been proposed by Holling (1992) and Zimov (1995).

#### Contribution to community ecology

Few, if any, studies in mammal community ecology involve as many species of as many different functional types as the present study. This is unfortunate since a complete picture should be built on the full set of species, especially if the ambition is to formulate general rules around the shaping and dynamics of species assemblages. I have shown evidence that functional types of mammal species may determine their responses to widely different environmental gradients, in the same time as their responses may have consequences for other mammal species, e.g. of other functional types. Even broader perception and deeper understanding could be achieved through studies including e.g. invertebrate soil faunas or whole biotas.

Another important message from my work is that there are similarities as well as differences between the structuring factors of mammal communities depending on spatial scale and biome. In the African savannas soil nutrient availability is an important environmental variable determining large- and medium-sized herbivore composition on a regional scale, while it is less important on a local scale. On landscape scale disturbance factors such as habitat depletion and competition are more important factors for the whole mammal community than soil nutrient variability. On a local scale small mammal assemblages are again highly structured by resource availability, in this case cover and thus probably also from the effects of predation. Most of the species and functional structures of the mammal community in the boreal forest ecosystem seems only superficially dependent on environmental variables on landscape scale (exceptions include roe deer and hare), possibly because a small part of the variation in the boreal forest occurs on that scale, or because the animals are generalists and overall tolerant to most of the variability in the ecosystem. However, also generalists have preferences, especially herbivores, and I think that some, here unidentified, patterns of mammal community composition in the boreal forest are yet to be studied on a local scale. If the structuring processes in tropical savannas are different depending on spatial scale, there are good reasons to expect the same in the northern boreal forests.

### Implications for conservation

Functionally, most of the extant wild herbivorous mammals of the boreal forest biome stand quite far from our domestic herbivores. Those that resembled livestock, e.g. wild horse (*Equus ferus*), aurochs (*Bos primigenius*), wisent (*Bison bonasus*) and wild boar (*Sus scrofa*), have been exterminated, regionally or globally. Most researchers agree on that humans played a role in the extinction of these species (Barnosky *et al.*, 2004) and it is easy to imagine the combined negative effects from competition with livestock and hunting by humans that this wild fauna was exposed to. Very much alike what we describe and hypothesize in Paper I, derived from recent data.

Extinction is predictable (Brown, 1995), an important message for conservationists world-wide. It is fairly well known, that very large-sized herbivores, the so-called megafauna, are prone to go extinct (Owen-Smith, 1989), as well as large carnivores (Woodroffe, 2000). However, the odds of smaller and less charismatic wild mammals, especially those functionally resembling our domesticated species, may not look any better. Conservation actions should therefore not entirely be focused on saving so-called flagship species (i.e. charismatic species) from hunting and habitat loss. Instead, continuous monitoring of competitive relationships and population trends of livestock and wild mammals belonging to the same functional types should have high priority. First of all, wild species resembling livestock may (just as megaherbivores) contribute to the structuring and function of indigenous mammal communities. Also, survivors of this functional group may tell the story of their extinct relatives belonging to other regions or biomes of the world. Such information can probably answer many questions around the roles that the extinct species played in the communities which now function without them.

## Conclusions

I present proof that grouping mammal species together based on their responses to environmental variables, such as resource availability and disturbance, and describing them as communities may be highly useful. Community compositions, especially of functional types, have high applicability for research, since patterns of change in community compositions and distributions often are directly related to measurable abiotic heterogeneities or biotic relationships in the ecosystem and ultimately across different scales and biomes. By interpreting community characteristics in relation to resources and disturbances it is possible to make predictions regarding changes in the assemblages and more importantly formulate hypotheses regarding their causes. This is important information when planning the management and conservation of indigenous wild mammal communities in African savannas and elsewhere. Usage of few indicator species for investigating the effects of environmental variables on entire communities may be misleading and should be interpreted with caution.

My thesis also shows that the generality of rules and principles formulated for specific mammal communities in specific biomes may be greater than we think. I have started to connect the patterns from different fields of mammal community ecology and although most work in this field still remains, a conclusion so far is that the finer structuring of the savanna mammal community, compared with the mammal community of the boreal forest, most likely has multiple causes on several spatial and temporal scales. Certainly, due to differences in species richness and habitat structure, the diversity of structuring processes is higher in the savanna than in the boreal forest. However, my work indicates that thorough descriptions of community compositions in relation to environmental variables can identify generally occurring common causes of variability. One example is the

support found among boreal forest herbivores for the Jarman-Bell principle, which was formulated for African savanna ungulates.

## Future perspectives

One of the concerns regarding recent research in community ecology is a wide-spread ignorance of environmental gradients, such as those of temperature, moisture and soil chemistry, as determinants of community properties (McGill *et al.* 2006). Instead, focus has been on species interactions, such as predation and competition, which do not entirely explain the systematic change in community compositions across space (McGill *et al.* 2006). Understanding the function of environmental variables as determinants of species assemblages is crucial for formulating general ecological rules regarding community ecology. It is also a necessity for projecting long-term effects of global climatic change on natural communities.

I recommend that future research in community ecology center around multi-species approaches, including multiple functional types, also for those questions that are traditionally restricted to few-species relationships. For example, good understanding of competitive interactions among ungulates can only be achieved when knowing how predation patterns affect herbivores of different functional types (Grange and Duncan, 2006). Similarly, the biotic interaction milieus of communities are best viewed in the light of the environmental variables that contribute to the shaping of the communities (McGill *et al.*, 2006). General conclusions about mammal community functionality should therefore always be built on knowledge of how resource availability and disturbances contribute to the shaping of the community on different scales.

My data indicated that the Jarman-Bell principle applies to the mammal herbivore community of the boreal forest ecosystem. However, more thorough studies are needed in order to fully verify this, particularly studies that allow exact species densities, instead of indices, to be calculated and thus provide accurate measurements of e.g. metabolic biomass as  $\text{kg}/\text{km}^2$ . It would also be useful to compare the functional structure of herbivore

communities within two forested areas with different nutrient conditions, e.g. a nutrient poor coniferous forest with a nutrient rich deciduous forest. Not least, such a comparison would reveal if the differences in habitat structure between coniferous forest and agricultural land in fact are the major causes of the difference in herbivore species assemblages. If the largest herbivore, moose, avoids agricultural areas primarily due to the lack of shelter, this could affect the results and conceal patterns related to the metabolic properties of the herbivore community.

Finally, new approaches of additional rules and principles formulated for mammal community ecology would greatly improve our understanding of mammal assemblages as well as our efficiency of protecting them. The truth is probably that the functions of mammal communities are more similar than they seem to be, due to different species compositions, and consequently there are many lessons to be learned from historical and present day alterations and even collapses of community structures. The great challenge in the future will be to know how to set focus (e.g. on which spatial or temporal scale) so that the correct conclusions can be drawn from studies of multiple communities.

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