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Chapter 1: General introduction

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Landslapes with distinct vegetation mosaics often support high floral and faunal diversity and positively affect many ecosystems functions and services, due to their high structural diversity of the vegetation (see Box 1) (Olff et al. 1999; Adler et al. 2001). For example, vegetation mosaics often contain a relative high plant, bird and mammal diversity (Harris 1988; Best et al. 1990; Kollmann and Schneider 1999; Magura et al. 2001; Fischer and Lindenmayer 2002; Ries et al. 2004). Furthermore, the presence of vegetation mosaics positively affects many ecosystems services, such as recreational values and protection against invasive species or against the spread of disturbances such as fire and pathogens (Turner 1989; Adler et al. 2001; Diaz and Cabido 2001; Woodcock et al. 2011). Consequently, for optimal use of our ecosystems as biodiversity refuges and for providing stakeholders of ecosystems with ecological and socio-economic valuable ecosystem services, more knowledge about how vegetation mosaics are generated and maintained is needed.

Vegetation mosaics can be generated by anthropogenic, abiotic and biotic sources. Humans can create and maintain vegetation mosaics by mowing, cutting, coppicing and planting (Bakker 1989). Examples of abiotic forces are fire and wind, but also static sources, such as heterogeneity in geology or hydrology (Turner 1989). For instance, a heterogeneous distribution of water may generate vegetation mosaics as low-lying, wet patches may support a different plant community (Phragmites australis), while dryer patches may support another (e.g. shadow tolerant woodland). Large herbivores are a prime example of a biotic driver of structural diversity. Several studies have shown that large herbivores can play a key role in generating and maintaining structural heterogeneity (McNaughton 1984; Olff et al. 1999; Adler et al. 2001; Bakker et al. 2004; De Knegt et al. 2008; Laca et al. 2010).

Large herbivores can generate structurally diverse landscapes by hierarchical foraging and self-facilitation (De Knegt et al. 2008). Hierarchical foraging is the result of herbivores making foraging decisions on different spatial and temporal scales (Senft et al. 1987). When herbivores are allowed to move long distances, they can migrate seasonally within the regional ecosystems. In montane ecosystems large herbivores migrate in winter to lower altitudinal ranges, whereas in riverine ecosystems large herbivores tend to migrate in winter to the higher and drier grounds (Fryxell and Sinclair 1988; Wallis de Vries 1995). However, many European ecosystems are too fragmented and isolated for seasonal migration of large herbivores (Wallis de Vries 1995). Consequently, most herbivores are forced
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The heterogeneous effect of large herbivores on the vegetation due to hierarchical foraging is strengthened by the process of self-facilitation (De Knegt et al. 2008, Bakker 1989). Grazing often increases the quality of forage plants. In the short term because grazing stimulates the growth of new, highly nutritious shoots that have low fiber content (Anderson et al. 2007), especially in productive ecosystems (Kuijper et al. 2008). In the long term, grazing often favors short stoloniferous and rosette-forming plant species that have low fiber content that increases their quality (Díaz et al. 2007; Kuijper et al. 2008). Consequently, those patches (at small and large spatial scales) that are intensively grazed are more likely to be repeatedly grazed. Moreover, by increasing the quality in grazed patches, large grazers may facilitate smaller herbivores. Allometric relations between body size and metabolic rate and body size and gut capacity suggest that larger herbivores can survive on lower quality but require higher bulk intake diets while smaller species require higher quality, but sustain on lower bulk intake diets (Kleynhans et al 2011). This increase in food quality by grazing promotes the visitation rates by (small and large) herbivores in grazed patches even more.

The heterogeneous impact of large herbivores on the vegetation often creates vegetation mosaics of tall and short vegetation patches (structural diversity). Where the short intensively grazed patches are then often dominated by grazing tolerant stoloniferous (lawn-forming) grasses and rosette-forming plants, the tall less intense grazed patches are dominated by grazing avoiding or grazing defended plants (due to thorns, spines and chemicals), often with a tussock architecture (Díaz et al. 2007). The variation in plant size and architecture in these mosaics has a strong positive effect on the structural diversity of the vegetation (see Box 1). Moreover, the difference in herbivore visitation rates may alter the successional pathways between short and tall patches. For instance, tree recruitment is often inhibited in short and intensively grazed patches, but not in less frequently grazed patches (Bakker et al. 2004; Smit et al. 2006; Vandenberghe et al. 2009). The result is unsynchronized succession between patches forming a mosaic, where intensively grazed patches remain short and are dominated by stoloniferous and rosette-forming grasses (Díaz et al. 2007). In contrast patches that are less intensively grazed may develop into shrub or woodland (depending on seed dispersal, germination and survival of these woody plants) or remain dominated by tall forbs and tall grasses (especially in more isolated patches).

Although large herbivores can play a key role in generating and maintain structural diversity, they not always do so (Adler et al. 2001). A potential predictor for whether large herbivores may generate and maintain vegetation structural diversity may be the interaction with the other drivers of structural diversity, namely anthropogenic and abiotic sources. In most ecosystems the structural diversity in the vegetation is the result of the interaction of all three sources (human, abiotic and biotic) (Vera 2000). For example, humans may interact with large herbivore-based processes by affecting herbivore density by herding, culling or by removing or introducing predators (Beschta and Ripple 2009). Large herbivores may interact with abiotic heterogeneity, e.g. by grazing mostly in more
fertile soil patches (McNaughton 1984). The goal of this study is to gain more insight in how large herbivores can play a role in generating and maintaining structural diversity in vegetation in interaction with abiotic heterogeneity and different types of herbivore density control.

1.1 Outline of this thesis

This thesis is roughly divided into two parts. **Part I** (chapters 2, 3 and 4) focuses on the effects of low herbivore densities on the development of structurally diverse vegetation mosaics. In the ecosystems described in this part herbivore densities are kept low as the result of artificial top down control such as herding and culling. **Part II** (chapters 5 and 6) investigates how naturally regulated herbivore populations affect structural diversity, i.e. without (direct) human control of the herbivore population.

1.1.1 Part I Vegetation mosaics under low-intensity grazing

**Chapter 2** investigates the importance of spatial variation in abiotic factors (such as hydrology) for the formation and maintenance of short lawn and tall rough patches under low-intensity grazing by different-sized herbivores. To assess the importance of abiotic variation a spatially explicit model of partial differential equations was made. Incorporated in the model is herbivore size (small, medium, large), hierarchical foraging, clonal invasion by plants, and abiotic variation.

**Chapter 3** describes an experimental study that explores how the vegetation mosaics of short lawn and tall roughs affect the recruitment of thorny shrubs. Thorny shrubs play a keystone role in grazed ecosystems by defending non-protected plants from herbivory, in particular woody saplings. Shrub patches can, therefore, transform into woodland patches. However, the establishment of thorny shrub species in grazed ecosystems is poorly understood.

In this study we hypothesized that tall roughs facilitate thorny shrub saplings. Two well-known thorny shrub species: *Prunus spinosa* and *Crataegus monogyna*, were used. The experiment was done in one of the few remaining ancient wood pastures in the Netherlands, Junner Koeland near Ommen (52°32’N, 6°36’E) (Fig.1.1).

Grazing is known to increase small-scale species richness, but at larger scales the effect on species richness is less clear-cut (Olff and Ritchie 1998). **Chapter 4** explores how the interplay of abiotic heterogeneity and grazing induced vegetation mosaics may increase plant species diversity at different spatial scales. Larger-scale topographic heterogeneity (differences in elevation over a few meters) is considered as a potential predictor for whether grazing mosaics increase plant species richness. The study was performed on a salt marsh on the island of Schiermonnikoog in the Dutch Wadden Sea (53°47’N, 6°20’E) (Fig.1.1).

1.1.2 Part II Structurally diverse landscapes without human induced top-down control

**Chapter 5** describes a large exclosure experiment in the nature reserve the Oostvaardersplassen (OVP) (52° 26’ N, 5°19’E) (Fig.1.1), a novel ecosystem formed on a former sea-floor after embankment. The OVP has a unique management approach where, instead of regular culling to enforce top-down control over the large herbivore populations, a “hands-off” policy was chosen. In addition, none of the large herbivores are predated on at any
life stage, implying that the population size of large herbivores in the OVP are bottom-up regulated (by limited food availability in combination with harsh winter conditions). This has resulted in very high herbivore densities, towards the upper limit of commercial stocking densities, but without any artificial fertilizer application or supplementary feeding, or offtake of animals and animal products. The aim of this exclosure experiment was to assess the possibility for tree recruitment in the OVP for six woody species in different vegetation types, namely short lawn (mostly grazed during growing season) and tall reed rough (mostly grazed after the growing season), under different accessibility scenarios for large herbivores, in combination with soil disturbance (mimicking effects of wild boar).

Chapter 6 theoretically explores the relative importance of the interaction between different-sized herbivores and different-sized predators in generating periods of tall and short variation, i.e. temporal diversity in the structure of the vegetation. Body size affects many traits of vertebrate herbivores. Body size positively affects tolerance towards low quality forage and negatively affects tolerance towards low forage quantity. As a result large herbivores can facilitate small herbivores when the vegetation is composed of tall and low quality plant species, while small herbivores can potentially outcompete large herbivores on uniformly short vegetation. In addition, small herbivores are generally more vulnerable to predation. The interaction between different-sized herbivores and different-sized predators may generate altering periods of short vegetation with periods of tall vegetation, i.e. cyclical succession. A simple model of ordinary differential equations was made to test these hypotheses.
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Box 1: Structural diversity of the vegetation

Structural diversity of the vegetation is defined as the spatial variation in plant architecture and plant size (Radloff and Mucina 2007, Cromsigt et al. 2008). Plant species often are dissimilar in architecture and size when they belong to different functional groups (Lavorel et al. 1997; Levin 1998). For example, grazing avoiding plants are often tall and have a tussock growth form, while grazing tolerant plants often are short and have a stoloniferous or rosette architecture (Rosenthal and Kotanen 1994; Diaz et al. 2007). Hence, coexistence of different functional plant groups, such as short, grazing-tolerant herbaceous plants and grazing-avoiding woody plants have a strong positive effect on structural diversity (Olff et al. 1999). Furthermore, structural diversity is expected to increase if the differences in plant architecture and plant size are heterogeneously distributed in space. Spatial heterogeneity is generated when different functional plant groups are distributed in patches of various shapes and sizes (Bakker 1989, Palmer 1988; Olff and Ritchie 2002), with various transitions from one patch type to another, ranging from gradients to discrete boundaries (Ries et al. 2004). In terrestrial European temperate ecosystems, high structural diversity in the vegetation is attained when the landscape is comprised of a mosaic of short and tall grasslands, tall forbs, shrub thickets and different types of woodland from different cohorts (Olff et al. 1999; Vera et al. 2006), (Donato et al. 2011) and patches that have a high variation in shape and size (Palmer 1988; Olff and Ritchie 2002). These structurally diverse European landscapes are generally the result of, and maintained by, large herbivores, and are often referred to as half-open landscapes.

The importance of structurally diverse vegetation mosaics for ecosystem services

Structural diverse vegetation mosaics often support high biodiversity (Olff et al. 1999) and therefore are ideal as biodiversity hotspots. There are several explanations why structural diversity had a strong positive effect on biodiversity. Firstly, structural diversity has a strong effect on habitat diversity, which in turn is a strong predictor of plant and animal diversity (Recher 1969; Palmer 1994; Ricklefs and Lovette 1999; Báldi 2008). Secondly, structurally diverse landscapes support high biodiversity because of the relatively high proportion of edge habitats (or ecotones), i.e. the transition zones from one habitat/functional plant group to another (Harris 1988). Several studies have shown that edge habitats not only contain a high diversity, but also consist of high abundances of plants, birds and mammals (Harris 1988; Best et al. 1990; Kollmann and Schneider 1999; Magura et al. 2001; Fischer and Lindenmayer 2002; Ries et al. 2004). For example, bird, mammal and tree diversity is often higher along the forest-grassland edges than in grassland or forest patches alone (Kollmann and Schneider 1999; Magura et al. 2001). Thirdly, biodiversity is often higher in structurally diverse landscapes because isolated patches of the same functional plant group may be occupied by different species. Within a functional plant group, species that are competitively superior are likely to dominate within a patch and outcompete competitively inferior species. However, due to dispersal limitations, these competitively superior species may not be present in relatively distant patches. Consequently, in some isolated patches, species that are competitively inferior may dominate (Tilman 1994), thereby increasing biodiversity on the landscape level.
Generating structural diverse vegetation mosaics may thus create refugia for many (endangered) species. However, structural diverse vegetation mosaics often positively affect other ecosystem services as well. As structural diverse vegetation mosaics consist of different functional plant groups they positively affect the functional diversity of an ecosystem. Functionally diverse ecosystems have higher resource-use efficiency, higher primary productivity and an increased stability (Cadotte et al. 2011; Cadotte 2011). Functional diversity thus increases the quantity/availability of goods provided by ecosystems, such as lumber, fiber, fuel and food (Díaz and Cabido 2001). Moreover, functional diversity has also been shown to increase the quality of services, such as protection from invasive species and recreational value (Díaz and Cabido 2001; Woodcock et al. 2011). The high functional diversity in these vegetation mosaics also increases the multi-functionality of the ecosystem (Loreau et al. 2001; Gimona and Horst 2007; Hector and Bagchi 2007; Koniak et al. 2009, 2010), which may increase the total economic value (Costanza et al. 1997; Gimona and Horst 2007). Furthermore, as most ecosystems have many stakeholders, policy makers are recognizing the importance of optimizing the number of ecosystem functions, goods and services, instead of maximizing the yields of a few (Gimona and Horst 2007). By creating multiple benefits, and thus satisfying the majority of local stakeholders, strong social support for management is generated and willingness to obey the rules is increased (West et al. 2006; Ostrom and Nagendra 2006), which in turn likely positively affect the longevity, stability and resilience of ecological and socio-economic valuable ecosystems.

Landscapes with high structural diversity are scarce in Europe, but once were very common (Olff et al. 1999; Vera 2000). From the early middle ages - and maybe earlier (Svenning 2002; Bakker et al. 2004) - to the late 19th century, grassland-woodland mosaics were abundant in western lowland Europe. As these common grounds produced high amounts of biofuels, lumber and animal forage (for both livestock and game) they were highly valued by western European societies (Vera 2000). Due to the openness of these landscapes light demanding trees, such as pedunculate oak (Quercus robur) flourished, which in turn produced large quantities of acorns that sustained a large number of pigs. Furthermore, the openness of these landscapes also favored light demanding fruit trees (Kollmann and Schneider 1999), which promoted honey production. Only when these landscapes were privatized or nationalized they lost most of their stakeholders along with the structural diversity (Vera 2000). The few remaining half-open landscapes are now especially valued for their high aesthetics and biodiversity (Olff et al. 1999).

Agricultural field abandonment provides an opportunity to again increase the amount of ecological and social-economic valuable vegetation mosaics in Europe that benefit many local stakeholders (www.rewildingeurope.com). In Europe, abandonment of agricultural fields has been an ongoing trend since the 1950s, generating several ecological and socio-economic problems, such as loss of biodiversity, large wild-fires and loss of local income (Kollmann and Schneider 1999; MacDonald et al. 2000; Moreira and Russo 2007; Cramer et al. 2008). For instance, nature conservation and tourist organizations may benefit from the high biodiversity, aesthetics, game densities and recreational value. Furthermore, these abandoned landscapes may be used for the production
of organic meat (livestock and game), particularly as the demand is increasing in the Netherlands and other Western European countries (Verhoeef 2005; Fairlie 2010). Adjacent fruit growers may also benefit from the high density of (natural) pollinators, while beekeepers may profit from the high density of flowering plants (Koniak et al. 2009, 2010). All the while the high structural diversity of these vegetation mosaics reduces the spread of disturbances, such as wild fires and pathogens (Turner et al. 1989). By providing many (local) stakeholders with such benefits, these structural diverse landscapes may remain a hotspot for floral and faunal diversity even if the trend in agricultural abandonment is stopped and reversed in Europe, as expected to happen with an increasing world population.