In this thesis I tried to gain more insight in how large herbivores can generate and maintain structurally diverse vegetation mosaics in interaction with abiotic heterogeneity and herbivore density control. In Part I of this thesis I focused on how structurally diverse grassland-woodland mosaics may be generated and maintained by low-intensity grazing (due to regulation of herbivores densities) (chapter 2 and 3). Furthermore, I investigated the effect of herbivore induced vegetation mosaics on species richness at different spatial scales (chapter 4). In Part II I focused on herbivore populations that were naturally regulated, i.e. without any human control of the herbivore population. In chapter 5 I investigated whether recruitment of woody species can occur with a bottom-up regulated herbivore community. Chapter 6 is a conceptual/theoretical study that investigated the role of different-sized predators and herbivores in generating and maintaining temporal structural diversity in the vegetation.

7.1 Main findings

7.1.1 Part I Vegetation mosaics under low-intensity grazing
Herbivores can generate and maintain vegetation mosaics. These vegetation mosaics generally consist of patches with lawn (dominated by short, high quality plants) and taller roughs (dominated by taller, low quality plants), and the high structural diversity of these mosaics has a strong positive effect on biodiversity and affects many ecosystem processes. However, the exact conditions required for herbivores to generate and maintain these vegetation mosaics are poorly understood. Chapter 2 investigated the importance of abiotic variation (e.g. spatial variation in water availability, salinity and soil oxygen) in interaction with herbivore body size for the formation and maintenance of vegetation mosaics. A spatially explicit model was made that incorporated herbivore size (small, medium, large), hierarchical foraging by herbivores, clonal invasion by rough plants, and abiotic variation. The results of our numerical solutions suggest that in the absence of abiotic variation, hierarchical foraging and clonal invasion, small herbivores (sheep-sized) are more likely to generate vegetation mosaics than large herbivores (cattle-sized). Large herbivores are less likely to generate mosaics as they tolerate low quality plant material and thus forage on tall patches with a relatively high-intensity. When hierarchical foraging and clonal invasion was added, small lawn patches are likely to merge into surrounding rough, as these small lawns are ignored by herbivores (as a side effect of hierarchical foraging) and invaded...
by clonal ramets from rough plants. Furthermore, small rough patches are accidentally grazed (also as a side effect of hierarchical foraging) and therefore are likely to merge in the surrounding lawn. This reduces heterogeneity in the long run as the emerging mosaic will only exists of a few large patches. Abiotic variation positively affects maintenance of the mosaic, because small rough patches that have a high growth rate can better cope with high grazing frequency, while small lawn patches with a low growth rate can better cope with low grazing frequency. Interestingly, the presence of abiotic variation also seems to increase the likelihood that large herbivores can form and maintain heterogeneous lawn-rough mosaics. Summarized, for formation of vegetation mosaics, abiotic variation seems more important in systems with large herbivores than with small herbivores. However, for maintenance of mosaics, abiotic variation is important with all herbivore sizes.

Chapter 3 studied the importance of patches of lawn and rough for the recruitment of thorny shrubs. Thorny shrubs play a keystone role in grazed ecosystems by defending non-protected plants against herbivores. Shrub patches can therefore transform in woodland patches. However, the establishment of thorny shrub species in grazed ecosystems is poorly understood. Biotic and abiotic factors were surveyed for saplings of thorny shrubs in plots with and without naturally established saplings. Plots with shrub saplings had taller surrounding vegetation, higher soil pH and higher soil moisture than plots without saplings. These plots predominantly contained low quality rough species, while plots without saplings mainly contained palatable lawn species. To disentangle these factors, a transplantation experiment was performed over two growing seasons with shrub saplings (*Prunus spinosa* and *Crataegus monogyna*) planted in tall, low quality roughs and short grazed, high quality lawns, half of them protected from herbivory via exclosures. After two years, sapling survival was higher inside exclosures than outside, and higher in tall rough exclosures than in lawn exclosures. Sapling growth was higher in tall roughs than in lawns, higher inside than outside exclosures, and higher for *Prunus* than *Crataegus*, while browsing on saplings was higher in lawns. Concluding: low quality tall roughs form an essential establishment niches for thorny shrubs in grazed temperate woodlands: they protect against herbivores before thorns fully develop in saplings, and sapling growth is better due to improved micro-environmental conditions. Once established and thorny, shrub saplings will grow out of the protective range of the roughs and in turn facilitate tree seedlings, which are essential for long-term persistence of grazed temperate woodlands.

Chapter 4 explored under which circumstances a grazing induced vegetation mosaic of short lawns and tall roughs increases plant species richness. The study was done on the salt marsh of the Dutch Wadden Sea island Schiermonnikoog, as strong variation in abiotic heterogeneity is found here. Larger-scale topographic heterogeneity (based on the standard deviation in elevation of a plot of 2200 m² with a 25 m² resolution) was hypothesized as a potential predictor for whether low-intensity grazing increases plant species richness. The results show that larger-scale topographic heterogeneity (based on a 2200 m², with resolution of 25 m²) positively affects species richness at all spatial scales measured (from 0.1 to 1000 m²) and that the effect of grazing to increase species richness depends strongly on the sampling area and the level of topographic heterogeneity. At small spatial scales we found that grazing always has a strong positive effect on species richness. At larger spatial scales the effectiveness of grazing to increase species richness depends strongly on topographic heterogeneity. At low topographic heterogeneity effectiveness of grazing on larger-scale species richness is highest. At intermediate topographic
heterogeneity, grazing is least effective and, even neutral at 1000 m². At high topographic heterogeneity the effectiveness of grazing is increased again. Thus, whether grazing has a positive impact on plant species richness depends on the abiotic heterogeneity present and the spatial scale at which impacts are studied. Consequently, low-intensity grazing can be an effective tool to increase small-scale species richness in grasslands. At larger spatial scales grazing is especially effective at low and high topographic heterogeneity. Grazing is probably not an efficient tool to increase species richness at intermediate topographic heterogeneity, but it does not decrease species richness either.

7.1.2 Part II Vegetation heterogeneity at different scales without human induced top-down control of herbivore populations

Chapter 5 investigated tree recruitment in the Oostvaardersplassen (OVP). The large herbivore community of this ecosystem, consisting of Heck cattle, Konik horses and red deer, is fully bottom-up controlled, as there are no large predators present and no active population regulation by humans takes place. This is therefore a suitable situation to study the consequences of high herbivore densities (metabolic biomass = 135 kg ha⁻¹) for the maintenance and development of structural diversity through woody species establishment. Saplings of 6 woody species were transplanted in 10 plots (5 in tall roughs, 5 in short lawns). Each plot contained three levels of accessibility to large herbivores: full access (no exclosures), limited access (1m tall exclosure), and no access (2m tall exclosure). In addition the soil was partly disturbed within each treatment (mimicking wild boar, which may be introduced in the area in the future). After two years, no saplings survived when large herbivores had full access, while sapling survival in the partial and full exclosures was 28 and 27.5%, respectively. Survival in the exclosures strongly depended on vegetation type, soil disturbance and woody species. Survival was higher in lawn than in rough, most likely due to reduced light competition. Furthermore, soil disturbance positively influenced the pioneer tree species. In conclusion, tree recruitment in the OVP is strongly limited by the bottom-up controlled herds of large herbivores. However, inside the exclosures survival is higher in lawn than in rough, suggesting that large herbivores have a positive indirect effect on tree recruitment in the OVP, as large herbivores create these lawns. Consequently, a fluctuating local herbivore density or the stimulation of grazing refuges through one-time manipulation of topography/hydrology (some additional ditches) are expected to accelerate the development of structural diversity in the OVP, if that is considered necessary.

Chapter 5 showed the potential importance of dynamical herbivore densities for tree recruitment in naturally grazed ecosystems. Chapter 6 assessed the potential importance of the interaction between different-sized herbivores and different-sized predators in generating periods of high and low herbivore density. 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 vegetation is composed of tall and low quality plant species, while small herbivores can outcompete large herbivores on short vegetation. In addition, small herbivores are more vulnerable to predation, as a small predator can only affect the smaller prey, whereas a large predator can affect both small and large prey. To explore how the combination of these traits affects the structure of ecosystems a simple model was made. Results of numerical solutions showed that starting with tall vegetation, large herbivores first increase in density and change the plant community towards a short grassland, which facilitates the presence of smaller herbivore species. When the small
herbivores reach high enough numbers, they reduce the densities of larger herbivores by outcompeting them. Due to the high density of small herbivores, the number of predators increases which over time reduced the density of small herbivores. This resulted in a period of overall low herbivore density, which reduced the pressure on the vegetation from herbivory, shifting the plant community from short, high quality plants to tall, low quality plants, resetting the system. Consequently, the interaction between different-sized herbivores and different-sized predators can generate cyclical succession in the plant community. Furthermore, the results show that for cyclical succession to occur, the presence of a small predator that only predate on the smallest herbivore is essential. The addition of a large predator, that predate on all herbivore species, is not essential, but it makes the occurrence of cyclical succession more probable.

7.2 Conclusion: Under which conditions do large herbivores generate structural diversity?

Landscapes 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 and 2 of chapter 1) (Olff et al. 1999; Adler et al. 2001). 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.

Structural diversity in the vegetation is often the result of anthropogenic, abiotic and biotic sources (Vera 2000). 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; Diaz et al. 2007; Cromsigt and Olff 2008; De Knegt et al. 2008). However, large herbivores do not always increase the structural diversity of the vegetation at all scales. The findings of this thesis suggest that whether large herbivores will realize this role depends strongly on the interaction with other sources of structural diversity, namely anthropogenic and abiotic sources.

The potential of herbivores to generate small-scale structural diversity in the vegetation depends strongly how herbivore density is regulated, often a direct (i.e. culling of herding) or indirect anthropogenic effect (introduction or removal of predators). When herbivore density is kept low by artificial means (i.e. herding or culling) structurally diverse landscapes, also at small spatial scales, may occur under a more relaxed set of conditions than when herbivore densities are regulated naturally (i.e. bottom-up regulation, or top-down regulation by predators).

When herbivore density is kept low by intervention, then abiotic variation seems to be an important predictor whether or not herbivores successfully generate and maintain a heterogeneous lawn-rough mosaic, especially with relatively large herbivores, such as cattle (chapter 2). For smaller herbivores, such as sheep, abiotic heterogeneity seems less important to generate abiotic heterogeneity, but remains important to maintain the heterogeneity of the mosaics. Furthermore, we found that when lawn-rough vegetation mosaics emerge, lawn and rough patches may show unsynchronized succession (chapter 3), form-
Herbivore-mediated structural diversity of vegetation

Herbivore-mediated structural diversity of vegetation (Olff et al. 1999; Vera 2000). Consequently, vegetation mosaics of tall rough and short lawn are the foundation for grassland-woodland mosaics. In turn, abiotic heterogeneity in soils and hydrology is an important prerequisite for the formation of mosaics of tall roughs and short lawns.

In the OVP, where the herbivore densities are bottom up regulated, little small-scale heterogeneous vegetation mosaics of lawn and rough are found (with a strong variety in patch size and shape). The strong uniform initial conditions under which this ecosystem started 40 years ago seem to be an important explanation for this. Nonetheless, even if a heterogeneous lawn-rough mosaic could establish, then under the current herbivore densities it will not rapidly develop into a grassland-woodland mosaic (chapter 5), as is the case when herbivore density is kept low by human intervention (chapter 3). Grazing refuges, such as woody debris, seem important for tree recruitment in ecosystems with such bottom-up regulation. An alternative potential mechanism that would increase recruitment of woody species is fluctuating herbivore densities, e.g. due to very harsh winters. This will have strong positive effect on tree recruitment, as at periods of high herbivore density lawns are generated, in which tree sapling survival is enhanced during periods of low herbivore density. These fluctuating herbivore densities may be generated by predation, but likely only when the predator community consists of both small and large predators (chapter 6). Also, abiotic heterogeneity in combination with temporal (climate) variability may contribute to tree recruitment events, for example when flooding restricts access of herbivores to some parts of the ecosystem during one or more very wet years. However, it should be noted that the OVP ecosystem is a novel ecosystem that is currently only 40 years old, which is probably still too little time for many of such biotically generated heterogeneity to arise, or very rare events to occur. Patience is needed here to see what happens and care should be taken not to directly compare this system to ecosystems that took centuries to millennia to develop their current diversity in vegetation structure.

Landscapes with a still high structural diversity have become scare across Europe (Olff et al. 1999; Vera 2000). The current agricultural field abandonment provides an opportunity to increase the amount of ecological and social-economic valuable ecosystems in Europe that benefit many local stakeholders (see Box 2, chapter 1). 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; Cramer et al. 2008). The findings of this thesis can contribute to the transformation of these abandonment agricultural fields into ecological and social-economic valuable landscapes and thus generating multiple ecosystem services. By creating multiple benefits, and thus satisfying the majority of stake-holders, 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 ecosystems.
Herbivore-mediated structural diversity of vegetation