Herbivore-mediated structural diversity of vegetation
Ruifrok, Jasper Laurens

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2014

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
English Summary

Ecosystems with high structural diversity of the vegetation often support high floral and faunal diversity and provide a large diversity of ecosystems functions and services. For a better use and management of these ecosystems more knowledge about how structural diversity of the vegetation is generated and maintained is needed. Large herbivores can play a key role in generating and maintaining structural diversity of the vegetation; however they not always do so. The goal of this thesis is to gain more insight in how large herbivores can play a role in generating and maintaining structural diversity in the vegetation.

In the first two chapters (2 and 3) I focus on how structurally diverse vegetation mosaics may be generated and maintained by low-intensity grazing, with the herbivore population size under human control. First, I investigated under which conditions different-sized herbivore can generate and maintain vegetation mosaics (chapter 2). These herbivore mediated vegetation mosaics generally consist of patches with lawn (dominated by short, high-quality plants) and roughs (dominated by tall, low-quality plants). I made a spatial explicit model to assess the importance of herbivore body size and abiotic heterogeneity. Incorporated in the model is herbivore size (small, medium, large), self-facilitation (grazing promotes the quality of forage plants), hierarchical foraging by herbivores (foraging decisions on different spatial and temporal scales), clonal invasion by rough plants, and abiotic heterogeneity (variation in soil moisture, soil oxygen, soil acidity or soil salinity). The result of our model showed that abiotic heterogeneity is an important predictor whether or not herbivores successfully generate and maintain a heterogeneous lawn-rough mosaic, especially with relatively large herbivores, such as cattle. 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.

Next I performed a descriptive and experimental study to investigate how succession differs between lawn and rough patches (chapter 3). I performed this study in one of the few remaining ancient grazed wood pastures in the Netherlands, Junner Koeland near Ommen. I found that lawn and rough patches show unsynchronized succession. In lawn patches recruitment of woody species is inhibited whereas rough patches form essential establishment niches for thorny shrubs: they protect shrub saplings against herbivores when their thorns have not yet developed. Furthermore, sapling growth is better in rough patches due to better micro-environmental conditions. Once established and thorny, shrub saplings grow out of the protective range of the rough patch and in turn may facilitate tree seedlings. Consequently, vegetation mosaics of tall rough and short lawn are the foundation for grassland-woodland mosaics. In turn, abiotic heterogeneity in the soil is an important prerequisite for the formation of mosaics of tall roughs and short lawns.

In the next chapter (4) I explored how plant species richness is affected by abiotic heterogeneity at different spatial scales in herbivore mediated lawn-rough mosaics. The study was performed on the salt marshes of the island Schiermonnikoog in the Dutch Wadden Sea, where abiotic heterogeneity is strongly linked with topographic heterogeneity. The results show that at small spatial scales, species richness is higher in grazed lawn-rough mosaics than in ungrazed sites. At larger spatial scales, at low and high topographic
heterogeneity, species richness is higher in grazed lawn-rough mosaics than in ungrazed sites. Yet, at intermediate topographic heterogeneity there was little to no effect on plant species richness. 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. Low-intensity grazing is probably not an efficient tool to increase species richness at intermediate topographic heterogeneity, but it does not decrease species richness either.

In the last two chapters (5 and 6) I focused on herbivore populations that are naturally regulated, i.e. without significant human control of the herbivore population. First, I investigated tree recruitment in the Oostvaardersplassen (OVP) (chapter 5). The large herbivore community of this ecosystem consists of Heck cattle, Konik horses and red deer, and is fully bottom-up controlled as there are no large predators present and no active population regulation by humans takes place. I performed a large transplantation experiment with 7000 saplings of 6 woody species. We selected ten plots; five plots were located in lawn vegetation, while five plots were located in rough vegetation. Within each plot saplings were planted in fully accessible (no fencing), partly accessible (1m high fence), or not accessible subplot (2m high fence). Within each subplot part of the soil was tillaged to mimic wild boar (which may be introduced in the area in the future). After two years I concluded that tree recruitment in the OVP is strongly limited by high-intensity grazing and trampling. While species differ in their responses, survival inside exclosures is generally higher in initial lawn vegetation than in initial rough vegetation. This suggests that large herbivores have a positive indirect effect on tree recruitment in the OVP, as lawns were created by large herbivores. Consequently, fluctuating herbivore densities in time (due to population crashes) or space (due to temporal inaccessibility) are expected to accelerate the development of structural diversity in the OVP, if that is considered necessary.

Next I investigated how fluctuations in herbivore density in time may be generated by the interaction between small herbivores (e.g. geese), medium herbivores (e.g. red deer) and large herbivores (e.g. bison, cattle or horses) and their vulnerability to predation by mesopredators (e.g. fox) and top predators (e.g. wolves). I made a simple model in which herbivore 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 (rough vegetation), while small herbivores can outcompete large herbivores on short vegetation (lawn vegetation). In addition, small herbivores are more vulnerable to predation as a mesopredator can only affect the smaller prey, whereas a large predator can affect both small and large prey. Results of model showed that the interaction between different-sized herbivores and different-sized predators can generate cyclical succession: periods of high herbivore density, and thus low tree recruitment chances, alternate with periods of low herbivore density and high tree recruitment chances. Furthermore, the results show that for cyclical succession to occur, the presence of a mesopredator that only predates on the smallest herbivore is essential. The addition of a large predator, that predates on all herbivore species, is not essential, but it makes the occurrence of cyclical succession more probable. However, whether the introduction of a large predator (e.g. wolf) would indeed generate such periods of enhanced tree recruitment in for example the Oostvaardersplassen would need empirical testing.
In conclusion
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). Depending on abiotic heterogeneity and herbivore body size, low-intensity grazing can result in heterogeneous lawn-rough mosaics, that generally hold relatively high (plant) species richness. Furthermore, patches of lawn and rough vegetation may show unsynchronized succession, which in turn may transform these lawn-rough mosaics in heterogeneous grassland-woodland mosaics. In the OVP, where the herbivore densities are bottom up regulated, little small-scale heterogeneous vegetation mosaics of lawn and rough exists. This may be partly explained by the strong uniform initial conditions under which this ecosystem started 40 years ago. Nonetheless, even given much heterogeneous lawn-rough mosaics in the OVP, the development of grassland-woodland mosaics is not very likely under the current high herbivore densities. Fluctuations in herbivore density in time (due to population crashes) or space (due to temporal inaccessibility), seem important for tree recruitment in ecosystems with such bottom-up regulation. A possibility to generate these fluctuations in herbivore densities is by predation, particularly when the community consists of both small and large predators.

Landscapes with high structural diversity in the vegetation once were common across Europe, but have become scarce due to massive land-use changes. The findings of this thesis provide useful insights that may contribute to successful generation and maintenance of structural diverse ecosystems with high ecological and social-economic value.