The battle between bioturbation and biocompaction
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Synthesis and Discussion

Ruth A. Howison
In this thesis I concentrated my efforts to two grazing ecosystems i.e. the north-west European temperate salt marshes and the African savannah. Here I will provide a short overview of our main findings, a framework of recommendations for future research and some general conclusions.

**MAIN FINDINGS**

**Chapter two** introduces a conceptual framework that integrates bioturbation by soil fauna into grazer-induced heterogeneity in vegetation structure (Fig. 7.1). This novel mechanistic framework improves our insight on how herbivores affect the key determinants of plant community composition, and it has important implications for the predictions of how grazing systems may respond to global change in terms of large-scale overgrazing or extreme droughts. In the following three chapters empirically and experimentally explore the importance of bioturbation in generating different vegetation structural types, in the presence of strong environmental forcing (i.e. tidal inundation gradient - Dutch salt-marshes (chapter 3 and 4), steep rainfall gradient - South African savannah (chapter 5 and 6) and extreme seasonality - both study regions).

**Chapter three** reports results of an extensive study on the Dutch barrier island salt-marsh of Schiermonnikoog, quantifying the species composition, morphological traits and physical soil conditions of structurally distinct vegetation patches (Fig. 7.1(i),(ii) – tall and lawn plant communities), under different grazing treatments (with and without large herbivores) and situated along a continuous tidal inundation gradient. Tall patches were dominated by the physically defended plant species *Juncus maritimus*. The study explores how strong physical defence traits by an individual plant species can facilitate a range of other grass species under intermediate consumer pressure by large herbivores. Besides refuge effects (Fig. 7.1(iii) – patch avoidance) I found that the reduced grazing pressure by large herbivores additionally facilitated soil macrodetritivores which profit both from the tall litter producing vegetation and their own positive feedback on soil amelioration which promotes tall thicker rooted plants (Fig. 7.1(i) – positive feedbacks generated through bioturbation). Our explanation extends from the individual plant-plant interaction scale to the landscape scale where large grazer induced abiotic stress and light stress form the main determinants of plant community configuration, with less impact of the tidal inundation gradient.

**In chapter four** I experimentally explored how litter feeding macrodetritivores alter the competitive balance between two salt-marsh grass species. *Festuca rubra* and *Elytrigia atherica*. *F. rubra* establishes early on in the succession of the salt-marsh and *E. atherica* establishes much later on, where these two species are found competing for the same position. We found that under more benign conditions the addition of soil macrodetritivores ameliorated soil conditions through bioturbation and promoted above ground biomass production (Fig. 7.1 – positive feedbacks generated through bioturbation). However at high environmental stress (waterlogging) the macrodetritivores became selective herbivores promoting *Elytrigia* over *Festuca*. Thus, the ecological role of macro-
Figure 7.1 Placing the respective chapters of this thesis into the conceptual framework proposed in Chapter 2.

(i) Bioturbation maintains tall vegetation through positive feedbacks on water and nutrient availability (Chapter 3 and 5).

(ii) Trampling and compaction induced by large grazers decreases soil macroporosity and promotes lawn abundance (Chapter 3).

(iii) Patch conversion mechanisms provide important information on how the temporal dynamic shifts between lawn and bunch grass patches occur (Chapter 3, 4 and 6).

A) Increased canopy density may be induced through ameliorated soil conditions and at extreme stress may be explained by 1) facultative and 2) highly selective grazing by litter feeding macrodetritivores (Chapter 4).

B) Patch avoidance through physical defence mechanisms (Chapter 3) or herbivore fecal deposits (Chapter 5) promote the aggregation bioturbing soil macrodetritivores.

C) Herbivores differing in body size, metabolic requirements, mouth morphology promote short and long term changes in vegetation structure and composition with important impacts over the short term (mesograzers) and long term (large grazers) (Chapter 6).

D) Mounding activity, which involves the redistribution of fine particulate B horizon clays to the soil surface by soil macrofauna, promotes lawn formation (not included in this thesis).

detritivores as facultative herbivores in addition to their classic role as decomposers deserves further attention.

In chapter five I experimentally tested the hypothesis of patch reversal from a short lawn community to a tall bunch community in an African savannah, through the mechanisms of patch avoidance. Herbivores with a body mass of >500kg defecate large quantities of fecal biomass in a single event, which remains on the soil surface for long periods of time. Previous studies have shown that herbivores avoid fecal deposits (Fig. 7.1(iii), patch avoidance), thereby reducing grazing and trampling pressure. We found a uniform significant effect, for both increased tall bunch cover and biomass and changes in soil structure (water infiltration and organic matter) induced by the dung treatments and which were independent of the rainfall gradient. We conclude that coprophagous macrodetritivores interact with large herbivores in contributing to the maintenance of structural heterogeneity in the vegetation of grazing ecosystems, with a special role of tunneling dung beetles. Especially the bioturbating activities of aggregated soil macrodetritivores may be a key component in generating structural heterogeneity in grazed ecosystems.
Different sized herbivores partition forage resources and thereby co-exist, however it is little known how these differences in feeding strategies impact vegetation structure and composition (Fig. 7.1(ii) – large herbivores). In chapter six we report on a large 10 year exclosure project conducted in the South African savannah. We specifically aimed to disentangle the effects between groups of different sized herbivores and interplay with regular anthropogenic fire and rainfall on vegetation structure and composition. We found that total grazing pressure of all grazers together was responsible for changes in vegetation height, however ungulate community composition best explained the functional community composition of grasses. Specifically, on the short term, smaller ungulate species (‘mesograzers’) had the strongest effect on vegetation composition, by shifting communities towards dominance by species with low specific leaf area and low nutritional value. In the long term, large grazers had stronger effects, with similar effects (dominance of species of low nutritional value and thin leaves). Surprisingly, the largest 'mega-grazer', white rhinoceros, did not have strong effects on the vegetation structure or composition.

Our results support the idea that different size classes of grazers have different effects on the functional composition of grassland plant communities. Therefore, the decline in the diversity of ungulate communities as happening worldwide is expected to have (had) major impacts on community composition and functioning of grassland ecosystems, even if total grazing pressure has remained constant, e.g., due to replacement by livestock.

SCALE OF HETEROGENEITY

In this thesis, focus was on the combined impacts of abiotic conditions and biotically imposed changes to these conditions through bioturbating soil macrodetritivores and large grazing herbivores on plant-plant interactions and resulting changes in plant community structure. Here we consider how the scale of patch heterogeneity may influence the dynamic shifts between different patch types. The importance and scale of vegetation heterogeneity is likely to vary along environmental gradients and spatial scales. Environmental forcing, i.e. gradients in rainfall, geology and temperature, determine regional species composition (Olff et al., 2002). At the landscape scale patchiness may range from coarse to fine grain (Fig. 7.2), which determines the connectivity between patches and opportunities for patch conversion mechanisms that enable shifts from one state to another (tall to lawn or lawn to tall). In benign conditions alternating vegetation types are driven by high productivity and coarse scale topographic features such as aspect (Phillips, 1995) or coarse scale disturbances such as fire (Van Langevelde et al., 2003), thus opportunities for patch conversion mechanisms are more limited because of the large distances required to move from one patch type to another (Fig. 7.2A). Under more stressful conditions, patch coarsening occurs because only species adapted to harsh conditions are able to persist (Bertness and Callaway, 1994, Phillips, 1995). In addition, locally high grazing intensity by large herbivores also promotes coarse landscape resolution, where trampling evens out small variations in local topographic heterogeneity (Van Langevelde et al., 2003, Mikola et al., 2009) (Fig. 7.2A). Fine scale grain is found at inter-
mediate rainfall and intermediate grazing pressure (Phillips, 1995) (Fig. 7.2B). These are conditions where patch conversion mechanisms dominate (Chapter 2), resulting in a dynamic environment where energy and nutrients are exchanged more frequently and patches shift from one state to another. Therefore, biocompaction-driven vegetation types can increase in abundance when external conditions change (years with lower rainfall), when internal conditions change (when herbivore herds decide to move elsewhere) or through an interplay between external and internal conditions. Thus, the magnitude and scale of biotically created vegetation heterogeneity depends on the spatial scale, type of ecosystem, the herbivore and soil fauna community and the magnitude to which soil structure (soil macroporosity) and local abiotic conditions can be altered.

**FUTURE RESEARCH**

In Chapter 2 we provide a global prediction on where we expect bioturbation-biocompaction patchiness to be important and suggest that macrodetritivores are undervalued in their ability to restore degraded landscapes. Specifically, I would highly recommend further investigations into patch conversion mechanisms with particular emphasis on the rate of patch reversal and duration of alternative stable states of lawn and bunch grass vegetation in different and geographically separated ecosystems.

We have conducted one of the first studies to combine multiple interacting abiotic stressors and multiple plant-plant interactions (Chapter 3), with the inclusion of biotically induced consumer pressure (Soliveres et al., 2015). This is an important advance for
facilitation research. Since in our study we show that broadening the study approach beyond plant pairs responding to single stress gradients, we gained important insight of how plant interactions at the local scale generate patterns in patchiness at the landscape scale. This was especially evident where the activities of soil macrodetritivores and large grazers had important impacts in changing local abiotic conditions, which was profitable for some plant species and detrimental for others. I would highly recommend comparative studies in different grazed ecosystems, thus providing the foundation for a meta-analysis that will enable plant interaction theory to extend across scales of ecological organization.

Further, benefactor species provide opportunities for other plant species to establish and persist in otherwise unfavorable habitats (Bruno et al., 2003). However less focus has been placed on the effects this has on the benefactor itself. Costs to benefactors could be gradual replacement of the benefactor by beneficiary plants through competition for nutrients and light (Tilman, 1990). I would suggest the following as a case study. 

*Juncus maritimus* provides niche opportunities for less grazing tolerant species (e.g. *Elytrigia maritima*) on temperate salt marshes (Chapter 3). However, over time *E. atherica* competes with *J. maritimus* for space. *J. maritimus* is then pushed towards the outer edge of the patch. This is a costly competitive replacement since cattle which prefer to graze on *E. atherica* then increase grazing pressure, which then leads to the replacement of *E. atherica* by *Puccinellia maritima* the short statured grazing tolerant grass species. 

*P. maritima* is again reinvaded at the tall patch front by *J. maritimus* through underground rhizomes. *P. maritimus* is a light demanding plant species and is therefore replaced by the taller *J. maritimus* through competition for light. For this research I would suggest a modeling approach following a rock paper scissors serial replacement of the 3 dominant grass species – through mechanisms of plant traits. To calculate the rate of change and gain insight into patch dynamics I would recommend digitizing patch boundaries from a time series of aerial imagery, spanning at least 30 years, and compare actual dynamics to alternative modelling scenarios.

Facultative grazing by litter feeding macrodetritivores is receiving increased attention in the literature (Chapter 4, Griffith et al., 2013). Since soil macrodetritivores are integral to soil formation processes and have now been shown to have unprecedented impacts on vegetation structure and community composition (Chapter 4). Further attention on these alternative feeding strategies is recommended. For example, to gain further insight into whether these alternative feeding strategies are generally applicable across different species of macrodetritivores and ecosystems, as an adaptive response to cope under extreme environmental stress and altered food resources.

Additionally I would recommend the use of grazing exclosures, over longer time periods, in the patch reversal - herbivore fecal deposition study (Chapter 5). Since we conducted our experimental manipulations in the presence of large grazing herbivores, we were not able to fully separate the mechanisms whereby bunch successfully replaced lawn vegetation – e.g. we propose that bunch grasses replace lawn grasses as a consequence of herbivores avoiding the immediate vicinity of fecal deposits thereby reducing exposure to pathogens, however selective removal nutrient enriched lawns growing adjacent to dung piles may also have played an important role.
CONCLUSIONS

Grazing ecosystems that support high structural diversity provide more opportunities for species co-existence across trophic groups and hence are expected to host a higher biodiversity. With increasing pressure on global resources for human food security and industry (Vitousek et al., 1997) as well as global climatic fluctuations (Lorenzen et al., 2011), we are increasingly required to rationalize our knowledge on the key mechanistic drivers. With this thesis: Chapter 2) provide a novel framework where the positive feedback of bioturbating soil macrodetritivores on vegetation structure could be formally integrated into grazing ecosystem theory, Chapter 3) investigate interspecific differences in plant traits and response to grazing by large herbivores, Chapter 4) experimentally quantify the mechanistic nature whereby soil macrodetritivores may alter plant-plant interactions, Chapter 5) experimentally invoke patch conversion to tall bunch grass through promoting aggregation of bioturbating coprophagous macrodetritivores, and Chapter 6) quantify the consequences for vegetation structure and composition through short and long term impacts by different groups of meso-, large and megagrazers.

Greater diversity of both grazers and vegetation types is important for understanding the responses of the system to major disturbances as fires, droughts and disease outbreaks (Seifan et al., 2011, Luck et al., 2003). As grazed ecosystems are expected to be among the most susceptible to future changes in climate and land use, a greater understanding of their structure and functioning is crucial (House et al., 2003, Sankaran and McNaughton, 1999). Regime shifts in grazing ecosystems are less likely to occur in response to human-mediated disturbances when a greater diversity of vegetation and grazers is present (Folke et al., 2004). The results of this study thus shed important light on how the interplay of abiotic stress gradients, grazers, plants and macrodetritivores contributes to ecosystem resilience.