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Herbivore species and density affect vegetation-structure patchiness in salt marshes

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ABSTRACT

The importance of spatial patterns for ecosystem functioning and biodiversity has long been recognized in ecology. Grazing by herbivores is an important mechanism leading to spatial patterns in the vegetation structure. How different herbivore species and their densities affect vegetation-structure patchiness is, however, poorly understood, and very few studies have simultaneously incorporated the underlying abiotic patterns. We investigated how different herbivore species and densities affect vegetation-structure patchiness. We conducted an experiment in a semi-natural grassland using horses and cattle in two densities each (0.5 LU/ha and 1.0 LU/ha). Transects of 25 m in length were positioned within the study salt marsh, and canopy and canopy height and soil elevation were measured every 25 cm to explore patterns in canopy height. Geostatistical variogram models were fitted to all transects with the elevation as a covariable to correct for the underlying abiotic patterns. The range (as a measure for patch size of short or tall canopy) and sill (as a measure for heterogeneity) of the variogram model were compared between horses and cattle and between two densities. Canopy height was lower in horse-grazed compared to cattle-grazed treatments and lower in higher herbivore densities. Patch size (range) (tall and short canopy) was significantly larger in horse-grazed treatments, and a trend of larger patch size was found for higher densities with both herbivore species. While herbivore species had no clear effect on heterogeneity, a trend of a higher heterogeneity (sill) was found in low densities. We found that the two herbivore species and densities have differential effects on canopy height, patch size and heterogeneity. Although some of these results were only found as trends, our study has important implications for conservation management of grazed salt marshes. To form heterogeneous small-scaled vegetation patterns we would generally recommend applying grazing with (1) cattle rather than horses, and (2) at low rather than high densities. We further discuss the relevance of our findings for other grazed ecosystems.

1. Introduction

The importance of spatial patterns in ecosystems has long been recognized in ecology (*e.g.* reviewed by Rietkerk et al., 2004; Rossignol et al., 2011). Spatial patterns can be an important factor allowing species to coexist and thus may increase biodiversity (Olofsson et al., 2008). Moreover, they could be used to assess the stability of ecosystems *e.g.* in arid regions, because certain patch formations can indicate an imminent catastrophic shift (Rietkerk et al., 2004). In nature three general types of patterns can be detected (Fortin and Dale, 2005): (1) trends or gradients, (2) patchiness and (3) randomness. Trends or gradients are generally found at large scales (kilometres), while randomness is mostly found at the smallest scales (centimetres). Patchiness is often detected at intermediate scales. A good example for patchy vegetation-structure is grazed grassland with typical and distinct co-occurring areas of short and tall canopy (*e.g.* Adler et al., 2001). While these patches clearly differ in canopy height, a random pattern is often found within these patches on smaller scales where short and tall canopy show no spatial autocorrelation. Spatial patterns emerge in different ecosystems and are induced by various mechanisms (Rietkerk et al., 2004). These mechanisms can be subdivided in plant-soil (*e.g.* Rietkerk et al., 2004) and plant-herbivore feedbacks (*e.g.* Adler et al., 2001). Plant-soil feedbacks are common in (semi-)arid ecosystems (Rietkerk et al., 2004), where plant roots increase the water infiltration rate and reduce the evaporation of water from the soil by shading. Thus, once present, plants increase the local availability of water compared to the surrounding bare ground, which leads to a distinct spatial pattern of vegetated and bare patches. Plant-herbivore feedbacks, and resulting spatial patterns, have extensively been documented in grasslands, where herbivores stimulate the productivity of grass by grazing and keep

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re-visiting the previously gazed patches of short, high-quality grass, resulting in the so called 'grazing lawns' (*e.g.* Adler et al., 2001; McNaughton, 1979, 1984). In contrast to the selective feeding on high-quality grazing lawns, the avoidance of tall reproductive grass or plant species with defence mechanisms can be another cause for patch formation (Rossignol et al., 2011). The avoidance of such plant species which possess defence mechanisms can facilitate non-defended plants (*e.g.* Smit et al., 2010), and is known as associational defence (Hay, 1986) or associational resistance (Smit and Ruifrok, 2011). The impact of grazing on grassland patchiness and biodiversity offers possibilities for nature management to apply grazing as a management tool (Metera et al., 2010). Whether grazing will indeed increase patchiness in grassland ecosystems (Adler and Lauenroth, 2000), depends on factors such as underlying abiotic patterns (Adler et al., 2001) and herbivore density (de Knegt et al., 2008). Also, the selectivity of herbivores (Adler et al., 2001), which might differ between herbivore species and densities, plays an important role in patch formation.

Information on the differential effects of different herbivore species on vegetation-structure patchiness is still scarce (*e.g.* Dumont et al., 2012; Knapp et al., 1999; Metera et al., 2010). The expected differences on the vegetation-structure patchiness might be caused by differences in selectivity and forage requirements among herbivore species. For example, generalists are expected to show random grazing patterns (Adler et al., 2001), but these random grazing patterns might not lead to the establishment of patchy vegetation-structure pattern. The selectiveness of herbivores is also directly linked to both nutrient (WallisDeVries et al., 1999) and total forage requirements (Duncan et al., 1990; Menard et al., 2002; Vulink and Drost, 1991). For example, cattle as ruminants require less food per day, compared to horses as hind-gut fermenters (Duncan et al., 1990; Menard et al., 2002; Vulink and Drost, 1991). Consequently, horses remove a higher amount of biomass per animal and are probably less selective. Therefore, horses compared to cattle are expected to produce a shorter canopy height and a less small-scaled vegetation pattern with a larger patch size of short canopy and lower heterogeneity.

In addition to herbivore species, the herbivore density greatly influences vegetation characteristics. An increase in herbivore density predictably causes a decrease in mean canopy height (Berg et al., 1997; Rossignol et al., 2011). The effect of different herbivore densities on patchiness is, however, more complex as herbivores are less selective in higher densities (Augustine and McNaughton, 1998). Berg et al. (1997) found that intermediate herbivore densities cause a pattern of short and tall patches with a high heterogeneity, while very high densities and the cessation of grazing caused a homogeneous short and tall canopy, respectively. Similar results were found in a model approach by de Knegt et al. (2008). A higher herbivore density leads to a higher removal of biomass (*e.g.* Berg et al., 1997; de Knegt et al., 2008; Kiehl et al., 2001). Therefore, higher herbivore densities are expected to generate a shorter mean canopy height. Furthermore, herbivores in higher densities probably become less selective and have to include un-preferred food items into their diet (Crawley, 1983). This may lead to few small-scale patterns and we would, therefore, expect the patch size of short canopy to increase and the heterogeneity to decrease in higher densities.

The described probable differences between herbivore species and herbivore densities on vegetation patchiness should be assessed carefully before the application of grazing as a management tool. Grazing for nature conservation is often applied in salt marshes along the coast of the Wadden Sea (Esselink et al., 2009) and here intermediate stocking densities were found to positively influence the plant-species richness (*e.g.* Bakker et al., 1993, 2003; Bos et al., 2002). It is assumed that a higher diversity is achieved in low stocking densities, because low densities create a patchy mosaic of short and tall vegetation. This mosaic enables grazing tolerant plants to grow in short patches and grazing sensitive plants to grow in tall patches and is therefore expected to lead to high total plant diversity. Salt marshes were traditionally used for livestock grazing at high densities (Esselink et al., 2000). However, in the past century the value of salt marshes as an important habitat for plants and animals was recognized and protected areas were installed (Kiehl et al., 1996). Due to regular inundations of seawater salt marshes are dominated by salt-tolerant plant species while trees are absent. Plant-species composition shows a clear zonation based on the elevation above mean high tide (MHT), which controls the flooding frequency and consequently is generally correlated with the most important abiotic soil characteristics like *e.g.* oxygen concentration in the soil (Davy et al., 2011). Hence, elevation, which can be easily measured for a large number of points, can be used as a proxy for soil characteristics in salt marshes. The marsh zonation reaches from the most frequently flooded lowest-elevated areas (pioneer zone), over the intermediate zone (low marsh) to the seldom-flooded, higher-elevated high marsh (Adam, 2002). Salt marshes along the Dutch Wadden Sea mainland-coast can be classified as semi-natural grasslands as they developed from man-made sedimentation-field structures (Esselink et al., 1998). They are therefore characterized by a regular pattern of straight drainage ditches rather than natural creeks.

To investigate how different herbivore species and densities influence vegetation-structure patchiness we conducted an experiment in two dominant plant communities of a salt marsh (low and high salt marsh zone) with a long grazing history. By including measurements of the soil elevation, we were able to exclude the effect of the underlying abiotic pattern on the vegetation and analyze the patterns induced by the animals. We expected to find differential impact of livestock species and herbivore density on the vegetation structure. More specifically, we expected the mean canopy height to be shorter (1a) in horse-grazed *versus* cattle-grazed grassland, and (1b) in grassland with higher herbivore densities. Furthermore, we expected the size of patches of short and tall canopy to be larger (2a) in horse-grazed *versus* cattle-grazed grassland, and (2b) in grassland with higher herbivore densities. Finally, we expected the spatial heterogeneity to be lower (3a) in horse-grazed *versus* cattle-grazed grassland, and (3b) in grassland with higher herbivore densities.

2. Materials and methods

2.1. Study area and set-up

The study area 'Noord-Friesland Buitendijks' is a temperate salt marsh situated at the northern mainland coast of The Netherlands (53°20′11″, 5°43′40″, Fig. 1) and is part of the UNESCO world heritage site Wadden Sea. The average yearly mean temperature is 9.5 °C and the average yearly precipitation is 820 mm (data Royal Netherlands Meteorological Institute). Local tidal amplitude is 2.1 m.

The study area was intensively grazed by cattle or horses for the past 20 years before the establishment of the experiment (Esselink et al., 2009). The experimental setup consists of two blocks, which are approximately 1.4 km apart. In 2010 we installed four different grazing treatments within each block; each grazing treatment in a paddock of approximately 11 ha. Treatments include grazing with either horses or cattle in low (0.5 LU/ha) or high (1.0 LU/ha) densities (Fig. 1). Similar herbivore densities were applied in a salt-marsh study by Andresen et al. (1990) and compared to a heavily grazed treatment (2.0 LU/ha) which we do not apply here because it was found to negatively impact diversity. Livestock was obtained from local farmers and grazing took place each year from May until