Biological Conservation 164 (2013) 150–157

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Grazed vegetation mosaics do not maximize arthropod diversity: Evidence from salt marshes

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ARTICLE INFO

Article history:
Received 25 December 2012
Received in revised form 8 April 2013
Accepted 25 April 2013
Available online 11 June 2013

Keywords:
Beetles
Habitat heterogeneity
Invertebrates
Patch grazing
Spiders
Grassland
Species richness

ABSTRACT

Light to moderate grazing in grasslands can create vegetation mosaics of short grazed vegetation and tall ungrazed vegetation. These mosaics have been proposed to maximize plant and animal species richness, yet experimental evidence, especially regarding arthropods is scarce. This study compares abundance, richness and species composition of arthropods in grazed mosaics to those of homogeneous short and tall vegetation.

We sampled arthropods on three German coastal salt marshes where grazing with three densities (high, moderate and none) was installed in 1989 on previously intensively grazed plots. Stable vegetation mosaics had developed under moderate stocking densities. We collected spiders, beetles, bugs and moth larvae by suction sampling in a stratified random sampling design.

Treatments had caused large differences in plant composition after 20 years, which were reflected in the arthropod community. Most species showed a clear preference for either short or tall vegetation, but some species were most abundant in grazed mosaics. Arthropod richness and composition were similar in patches of short vegetation in moderately and highly stocked plots, while patches of tall vegetation were similar to ungrazed plots. Surprisingly, however, grazed mosaics were not richer in species than homogeneous tall vegetation, despite the co-occurrence of species from short, tall and mosaic vegetation.

We conclude that, although arthropod richness of salt marshes is greatly enhanced when stocking density is decreased, this cannot substitute ungrazed marshes for conservation of arthropod diversity. However, long term cessation leads to the disappearance of several species, and therefore the possibilities of rotational grazing should be explored.

1. Introduction

European coastal salt marshes are productive grasslands subject to frequent flooding by sea water, and are of high nature conservation value because of their species-poor, but highly characteristic plant and arthropod communities. Grazing by large herbivores is often used as a tool in conservation management in salt marshes to maintain plant species richness and to create heterogeneity (Bouchard et al., 2003). While cessation of grazing leads to a dominance of tall grasses, under grazed conditions a more species-rich short vegetation is maintained (Bakker et al., 2003), facilitating small vertebrate herbivores such as geese (Bos et al., 2005). Under moderate to low stocking densities, stable mosaics of short, grazed vegetation and tall ungrazed vegetation develop (Berg et al., 1997; Versteegde, 2011). With respect to invertebrates, species richness of beetles, spiders and bugs increases after cessation of grazing, due to an increase in ubiquitous species, while under grazed conditions salt-marsh specialists dominate (Andresen et al., 1990; Pétillon et al., 2007; Ford et al., 2013). Moth communities, on the other hand, respond sensitively to grazing, and are only able to maintain species richness under very low stocking densities (Rickert et al., 2012).

The creation of a mosaic of short and tall vegetation can occur in almost any grassland type (Adler et al., 2001) if large grazers visit certain patches frequently (the so-called grazing lawn), while other

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http://dx.doi.org/10.1016/j.biocon.2013.04.023

patches are only grazed incidentally or remain ungrazed (McNaughton, 1984; Adler et al., 2001; Dumont et al., 2012). In several ecosystems these structural vegetation mosaics have been shown to be beneficial for species richness of plants (Olofsson et al., 2008; Marion et al., 2010) but studies of the effects on arthropods are scarce.

In general, high densities of large grazers are detrimental to arthropod species richness, and richness will increase when densities decrease (Morris, 2000). At low densities or in ungrazed situations, however, results are inconsistent. Many studies have shown a linear or asymptotic increase of arthropod richness with decreasing grazer density, with richness peaking in the absence of herbivores (e.g. Kruess and Tscharntke, 2002a,b; Öckinger et al., 2006). This is usually attributed to decreased disturbance (Kruess and Tscharntke, 2002a) or an increase in vertical vegetation complexity (Kruess and Tscharntke, 2002b), which is known to be one of the most important factors determining arthropod species richness (Luff, 1966; Lawton, 1983; Tscharntke and Greiler, 1995). Other studies found a positive effect of grazing on arthropod richness (e.g. Joern, 2005; Vulliamy et al., 2006), which was attributed to increased vegetation heterogeneity created by large grazers.

Most arthropod species show a specific response to grazing, with some species being more abundant in short grazed vegetation, while others are more abundant in tall, ungrazed vegetation (e.g. Dennis et al., 1997, 2001; Woodcock et al., 2007). A mosaic of short and tall vegetation should therefore optimize species richness. Yet, despite the generally positive relation between habitat heterogeneity and animal richness (Tews et al., 2004), evidence supporting this is limited.

For several thermophilous insects, vegetation mosaics consisting of a patchwork of short and tall vegetation have been shown to be essential to complete their life cycles (Cherrill and Brown, 1992; Roy and Thomas, 2003). At the community level Joern (2005) found a positive relation between vegetation heterogeneity and grasshopper species richness in prairie grasslands, but other studies did not find such a clear result. In grazed mosaics, patches of tall vegetation were found to be richer in arthropod species and individuals than patches of short vegetation (Cherrett, 1964; Dennis et al., 1998; Helden et al., 2010). Furthermore, species richness was negatively related to management intensity, suggesting that vegetation height rather than mosaic structure determines species richness (Dennis et al., 1998). This was supported by Helden et al. (2010) who found that the proportion of arthropods living in patches of tall vegetation decreased when the surrounding vegetation was taller. These studies, however, were conducted in short-term grazing experiments and effects of long term vegetation changes in these mosaics were not yet pronounced. Investigations of the long-term impact of patch grazing on arthropod communities are, therefore, urgently needed. We aim to fill this knowledge gap by comparing mosaics of tall, late successional vegetation and short grazing lawns created by 20 years of experimental grazing to homogeneous tall and short vegetation found under ungrazed conditions and intensive sheep grazing, respectively, in a salt marsh ecosystem.

We hypothesize that most arthropod species will show a clear preference for either short or tall vegetation, but that some species will peak in grazed mosaics (H1). The difference in arthropod communities of grazed and ungrazed salt marshes will be reflected in the species richness, abundance and composition of arthropod communities in structural vegetation mosaics (H2) (i.e. patches of short vegetation will resemble homogeneously short grazed vegetation, and patches of tall vegetation will resemble ungrazed salt marshes). Consequently, because of the co-occurrence of species associated with tall vegetation, short vegetation, and mosaics, grazed mosaics should sustain higher arthropod species richness than homogeneous vegetation (H3).

2. Methods

2.1. Study sites

This study was performed at three sites on the Wadden Sea coast of Schleswig–Holstein, Northern Germany (see Fig. S1). At these sites, experimental sheep grazing with three stocking densities (high: 10 sheep ha^{-1}, moderate: 3–4 sheep ha^{-1} and abandonment: 0 sheep ha^{-1}) has been maintained continuously for over two decades (Stock et al., 2005). The marshes were grazed throughout summer (May – October) and sheep were only removed during flooding events. All sites are man-made salt marshes, originally created for land reclamation using sedimentation fields, but are now part of the protected Wadden Sea National Park and UNESCO world heritage site.

The salt marshes of Friedrichskoog (FK) (54°02′N, 8°54′E, currently ~70 cm above mean high tide (MHT)) and Sönke–Nissen–Koog (SNK) (54°38′N, 8°50′E, currently ~40 cm above MHT), have been part of a grazing experiment that started in 1988. At each site, grazing regimes were established on adjacent paddocks that were intensively grazed until 1988 (~10 sheep ha^{-1}), stretching from the sea wall to the intertidal flats. For details on the experimental setup see Dierßen et al. (1994), Meyer et al. (1995). Each treatment level was present once at each site, but experimental units were large (11–15 ha). FK represents a typical higher salt marsh, where the grass *Festuca rubra* is the dominant plant species,while at SNK a typical lower salt marsh is found, dominated by the grass *Puccinellia maritima*. The salt marshes of the Hamburger Hallig (HH) (54°36′N, 8°50′E, currently ~55 cm above MHT) have been under stable grazing management since 1991, and are characterized by plant species of both high and low salt marshes (for details see Stock et al., 2005).

At each site, we investigated three different vegetation patterns that were created by grazing: high stocking densities (10 sheep ha^{-1}) maintained homogeneous short vegetation with many early successional plant species, no grazing (0 sheep ha^{-1}) led to late-successional homogeneous tall vegetation, and grazing at moderate stocking densities (3–4 sheep ha^{-1}) created a mosaic of patches of short and tall vegetation. The patches of tall vegetation were all similar in size (4–10 m^2) and were spaced at least 20 m apart, separated by one or more ditches. They covered maximum 30% of each 4 ha plot area, and had developed a distinctly different vegetation composition from the short grazed vegetation. The three treatments therefore represented four structural vegetation types: homogeneous short vegetation, homogeneous tall vegetation, and short and tall vegetation (referred to as "mosaic short" and "mosaic tall", respectively) at moderate stocking densities.

2.2. Sampling design

At each site, a representative elevation above mean high tide (MHT) was chosen as mean plot elevation matching with the dominant plant community, because elevation above MHT strongly influences arthropod community composition in salt marshes (Irmler et al., 2002). In each of the three paddocks per site, we established a plot of 200 m × 200 m. Each plot contained 16 sampling locations, at least 10 m apart and restricted to the mean plot elevation ±10 cm.

In plots with homogeneous vegetation, 16 locations were chosen with the following restrictions: distance between locations was at least 10 m, and due to the rigid ditching structure (spaced 10 m apart) typical for man-made mainland salt marshes, all sampling locations were separated by at least one ditch. The exact sampling locations were then randomly selected by throwing a stick downwind. In the vegetation mosaics we used a stratified random