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AGEE 5308 No. of Pages 17

ARTICLE IN PRESS

Agriculture, Ecosystems and Environment xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Rewilding with large herbivores: Direct effects and edge effects of grazing refuges on plant and invertebrate communities

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ARTICLE INFO

Article history:
Received 28 August 2015
Received in revised form 21 January 2016
Accepted 29 January 2016
Available online xxx

Keywords:
Exclosures
Null-model
Beta-diversity
Turnover
Diversity
Species richness

ABSTRACT

Natural grazing refuges can contribute significantly to plant and animal diversity in grazed ecosystems, particularly when herbivore densities are high. When natural grazing refuges are absent, artificial refuges could be created, for example by means of fencing. It remains, however, unclear how grazing refuges affect the diversity of various taxa in their surroundings. Edge effects can be expected to be positive for biodiversity because at these edges minimal disturbance is combined with beneficial light conditions for plant diversity. This can be expected to decrease with increasing distance and to differ between matrix vegetation types.

Here, we investigated the impact of herbivore exclusion through fencing on communities of plants and various invertebrate taxa in a rewilding area on very productive soil, the Oostvaardersplassen, The Netherlands. The area is grazed year round by Heck cattle, konik horses and red deer, at a combined density of approximately 2.4 animal ha^{-1}. Ten exclosures (13×12 m) were erected in 2010 and plant communities were monitored for three years. In the third year, pitfall trapping, earthworm counts and plant surveys were performed in the centre, at the edge, at 10 m and at 20 m distance from each exclosure.

Plant species richness declined strongly at the centre of the exclosures, but remained high outside the exclosures and at their edges. Earthworm, isopod, myriapod and ground beetle diversity increased in the exclosures, but showed small or no differences in species composition, while weevils showed a decrease. Spider, true bug, and leafhopper diversity did not differ, but showed large changes in species composition. For leaf-, dung and click beetles, neither diversity nor species composition differed systematically between treatments. For all taxa, diversity at the exclosure edges was as high as in the most diverse treatments, thus, combining all taxa to calculate multidiversity showed species richness to peak at the edge of the exclosures, but this positive edge-effect extended less than 10 metres.

We conclude that when natural grazing refuges are not present, the creation of grazing refuges may thus be an effective management tool to increase diversity. Because exclosure edges support the highest multidiversity, maximising the edge length will have most beneficial effects for grassland flora and fauna, which can be achieved by creating many small, rather than few large refuges, or by creating serrated rather than straight edges. Such positive effects can be expected to be beneficial to higher trophic levels such as birds and other vertebrates.

1. Introduction

Grazing by large mammalian herbivores has historically and prehistorically been a major structuring force in almost all terrestrial ecosystems (Bakker et al., 2015), affecting plant and animal communities. Grazing is under certain conditions beneficial to plant species richness (Milchunas et al., 1988; Olff and Ritchie, 1998), but is damaging to ecosystems and biodiversity when large herbivore densities are high (Côté et al., 2004; Morris, 1967; Smith, 1940). Herbivores can reach high densities in the absence of top down control, which can happen on isolated islands, after extermination of large carnivores, or among feral herds (e.g. Boyd et al., 1964; Smith et al., 2003). Under such conditions, the presence of grazing refuges is important for tree recruitment (Smit et al., 2006), maintenance of populations of grazing-sensitive plants (Chollet et al., 2013; Rebollo et al., 2002; Shitzer et al., 2007), and animal diversity (Foster et al., 2014; van Klink et al., 2015). Grazing refuges can be of geological (e.g. rock outcrops or water bodies) or

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http://dx.doi.org/10.1016/j.agee.2016.01.050
0167-8809/© 2016 Published by Elsevier B.V.

biological origin (e.g. spiny shrubs) (Milchunas and Noy-Meir, 2002).

In Western Europe, grazing by large herbivores is a commonly applied management type in nature restoration projects, which increasingly takes place on abandoned agricultural lands. Here, heterogeneity in abiotic conditions is typically absent, since agricultural practices have increased productivity and removed underlying geological and hydrological features (Benton et al., 2003). As such, abiotic grazing refuges are often not present, while also biotic refuges are typically absent through consistent historical removal. Biotic grazing refuges are characterized by the presence of chemically or mechanically defended plant species that can serve as protective structures for grazing-sensitive species. When protective species are present, spatial differentiation in grazing will occur where large herbivores will return to previously used feeding stations, while locations with chemically or mechanically defended plant species are avoided (Smit et al., 2006). An additional factor determining the emergence of biotic grazing refuges is the density of large herbivores. When herbivore densities are high, also defended species are unable to establish, decreasing the chances for their protégés (Smit et al., 2015) and grazing-sensitive fauna. This interaction between abiotic and biotic heterogeneity and the presence of grazing refuges is especially relevant in the context of rewilding, which in Europe is typically considered on such abandoned agricultural lands (Merckx and Pereira, 2014; Navarro and Pereira, 2012). The general aim of rewilding is to restore and maintain natural processes with minimal human intervention (Navarro and Pereira, 2012; Sandom et al., 2013), although interventions to push the system into the desired direction are usually implemented (Sandom et al., 2013). Typically, this involves reintroductions of keystone species, such as large herbivores.

In the absence of natural grazing refuges, artificial refuges, for example in the form of wildlife exclosures, water bodies, or coarse woody debris, can assume their role in protecting grazing sensitive plant and animal species (Beever and Brussard, 2000). These have been shown to be beneficial to species richness of gastropods (Suominen, 1999), spiders (Warui et al., 2005), herbivorous insects (Den Herder et al., 2004; Roininen et al., 1997), beetles (Barton et al., 2011), soil organisms (Wardle et al., 2001) and abundance of small mammals (Beever and Brussard, 2000). On plant diversity, contrasting effects of herbivore exclusion have been reported, mediated by site productivity (Bakker et al., 2006). Under nutrient-rich conditions, the exclusion of large herbivores can result in light competition among plant species, with a subsequent decline in plant species richness. Under nutrient poor conditions, competitive exclusion is expected to be less important in determining plant species richness (Bakker et al., 2006; Olff and Ritchie, 1998; but see Shitzer et al., 2007).

In contrast to the interior areas of grazing refuges, however, competitive exclusion among plant species can be expected to be of less importance at their edges. Here, disturbance through trampling and defoliation are minimal, while beneficial light conditions for plants are maintained. For invertebrates, this should result in an increased abundance and diversity of resources at these edges, caused by a tall-statured, species-rich plant community with a well-developed litter layer. Additionally, these transition zones will have a warmer microclimate than the exclosure interiors, while providing shelter from weather extremes and predators. Mobile species can also make use of resources both in- and outside the exclosures (Dennis and Fry, 1992; Ries et al., 2004). In analogy with forest–grassland ecotones (Ewers and Didham, 2006; Harper et al., 2005; Łuczaj and Sadowska, 1997) or crop–boundary ecotones (Saska et al., 2007), we thus expect overall diversity to peak at the exclosure edges and to decrease with distance from the exclosures. The magnitude of the edge effect is expected to depend on the contrast between the vegetation types (Harper et al., 2005).

In a highly productive rewilding area (Oostvaardersplassen, The Netherlands) with high densities of large herbivores (red deer, konik horses and Heck cattle), we tested two concrete predictions: (i) the effect of fencing out large herbivores on species richness (α-diversity) and species composition will differ between taxa, where plant diversity is expected to decrease, with a concomitant decrease in diversity of herbivorous taxa, while diversity of detritivorous taxa is expected to increase, followed by an increase in diversity of carnivorous taxa. Diversity of dung feeding species is expected to decrease under herbivore exclusion. (ii) The edges of the exclosures will be most species rich. These predictions were tested in two different, but adjacent vegetation types, which differed in vegetation height and composition: short grazed lawn (SL) vegetation and tall herbaceous (TH) vegetation. We assessed the response of plant, earthworm, soil macrofauna (myriapods and isopods), spider, plant-and leafhopper, true bug, ground beetle, dung beetle, click beetle, leaf beetle and weevil species richness and community composition, where we take an taxonomic rather than a functional approach to enhance comparability with previous and future literature, which usually focuses on one or a few taxonomic groups (van Klink et al., 2015).

2. Methods

2.1. Study site

The experiment was performed in the Oostvaardersplassen (OVP; N52°26′, E5°21′), a 5600 ha nature reserve located in the province of Flevoland, The Netherlands, which was embanked in 1969 and is surrounded by water on all sides. The site is located at some 5 m below sea level and has a temperate oceanic climate with a mean annual temperature of 10.1 °C and an average of 833 mm precipitation annually. Heck cattle (*Bos taurus*), konik horses (*Equus ferus caballus*) and red deer (*Cervus elaphus*), were introduced in the reserve in 1983, 1984 and 1992 respectively. These populations are not human-regulated, although an early-reactive management is applied to minimize animal suffering. Concretely, individual animals that are not likely to survive are shot, which typically occurs at the end of winter (ICMO2, 2010). Since their introduction, the herds have grown until a density of 2.58 heads per hectare (0.18 Heck cattle ha^{-1}, 0.61 Konik horses ha^{-1}, 1.79 Red deer ha^{-1}) in 2012 (Cornelissen et al., 2014b). These herds have decreased shrub cover and increased cover of homogeneous grassland (Cornelissen et al., 2014a,b; Vulink et al., 2000). This grassland is best described as productive, wet grassland on clay soil, dominated by nitrophilous grasses and forbs. In addition to the large herbivores, considerable numbers of geese visit the OVP during winter and early spring (predominantly *Branta leucopsis*, ca. 20,000), while (not introduced) Roe deer (*Capreolus capreolus*) and hare (*Lepus europaeus*) are currently very rare. The red fox (*Vulpes vulpes*) is the largest mammalian carnivore in the study area.

2.2. Experimental setup

In April 2010 (year 1), ten exclosures (13 m × 12 m) with adjacent control plots were erected in a 1 km × 1 km area in the south of the reserve. At this location, grazing by the large herbivores mainly occurs between October and May, when food is scarce. During the summer months grazing is concentrated in other parts of the reserve. The exclosures were placed in two SE–NW directed rows, divided over the two dominant vegetation types: the short lawn (SL) vegetation dominated by grasses (mostly *Lolium perenne*), and the tall herbaceous (TH) vegetation