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Do moose redistribute nutrients in low-productive fen systems?

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ABSTRACT

The reduction of human use in many grassland systems across Europe has led to bush encroachment and a loss of biodiversity. Low intensity grazing systems by livestock has often been used as a cost-effective management tool to counteract this process. However, not all semi-natural grasslands are suitable for this due to large distance from human settlements or adverse environmental conditions. In this study we address the question whether natural wild large ungulates can be a useful management tool as well. In nutrient-limited systems, large herbivores can affect vegetation dynamics by redistribution of nutrients next to their direct effects on the vegetation. They can preferentially forage plant species and deposit their pellets at other locations leading to nutrient redistribution. We studied whether moose (*Alces alces*) in the Biebrza National Park (Poland), plays a role in nitrogen dynamics. Microscopic analyses of faeces showed that 57% of the diet consisted of *Salix cinerea*, which was preferentially foraged upon indicated by a positive Jacobs' selectivity index. Pellet density was significantly higher in patches of *S. cinerea* compared to the surrounding vegetation. Based on the chemical composition of moose pellets and the pellet density, we calculated that moose-derived N (faeces and urine) leads to a relevant N-input in willow patches compared to other sources of N in the system. We show that moose do not redistribute nitrogen between different vegetation types but instead speed up the local recycling of nitrogen in patches dominated by willows during the growing season. As a consequence, nutrients become quicker available here than in other parts of the system. We hypothesize that enhanced N-availability in willow patches may off-set the growth reduction caused by moose browsing on willows, which fits to the observed continuous expansion of willows in the study area despite high density of moose. This suggests that moose likely stimulate the growth of willow rather than the often supposed suppression of this woody species. In these systems, more labour-intensive management (f.e. mowing) is required to counteract bush encroachment.

1. Introduction

Rich fens are severely threatened, both in Europe and N-America (Van Diggelen et al., 2006; Lamers et al., 2014), yet at the same time highly appreciated because of the high diversity of species adapted to such extreme environment. Hampered mineralisation rates make undrained fens low-productive, despite a huge stock of nutrients present in the soil (Wassen et al., 1996; Van Diggelen et al., 2006). At the same time this close coupling between water regime and nutrient availability renders these systems highly vulnerable to even slight drainage. Typical fen plants are then outcompeted by faster growing species (Kotowski et al., 2006) and the sites are colonised by shrubs and trees (Kotowski and Piorkowski, 2005).

As long as nutrient availability remains low, mowing or grazing by livestock can enable the survival of characteristic (often red list) fen plant species even under slightly drained conditions by preventing the dominance of tall growing shrubs or bushes (Van Diggelen et al., 2006). This used to be the normal situation in many wetlands in the temperate zone of Europe until mid-20th century but since then it became almost entirely restricted to regions in eastern Europe and the former Soviet Union with poor socio-economic development. However, after the collapse of communism, land-use intensity decreased substantially there and farmland abandonment and subsequent woodland expansion are now widespread (Kuemmerle et al., 2011; Prishchepov et al., 2012, 2013). Vast areas of abandoned wetlands in post-communistic Europe are nowadays rapidly losing their high conservation value. Reintroduction of mowing and/or low-intensity livestock

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grazing in no longer managed fens has been shown to be very effective for biodiversity conservation (Kotowski et al., 2013; De Mars et al., 1996), but is certainly not a panacea. In many sites agricultural management is highly uneconomical because of a large distance to human settlements or adverse terrain conditions that make access by machines or livestock impossible. In the present study we therefore address the question whether natural wild large ungulates can function as a substitute for human management in no longer managed fens and keep the nutrient availability so low that the endangered plant species can persist.

There is one large herbivore specifically associated with low-productive fens in the temperate zone, namely moose (*Alces alces*). Moose can occur at relatively high densities of up to 3 individuals km^{-2} (Gębczyńska and Raczyński, 1992) and could potentially have a large impact on vegetation dynamics. Several authors even assume that their impact is so large that moose are able to slow down or even stop bush encroachment in fens and other low-productive wetlands (Borkowska and Konopko, 1994; Middleton et al., 2006). Unfortunately, data about the effects of moose on vegetation dynamics in temperate fen systems are very scarce, this in contrast to boreal systems where they have been extensively studied. There they affect the ecosystems by suppressing the recruitment of certain tree species while accelerating the recruitment of others (Brandner et al., 1990; McInnes et al., 1992; McLaren and Peterson, 1994; Pastor et al., 1993). In addition to such direct effects at the plant level, indirect effects on nutrient cycling at the ecosystem level often seem to be even more important in boreal systems (Pastor et al., 1988; Kielland and Bryant, 1998). In many cases moose browsing slows down carbon and nutrient turnover during later successional stages (Pastor and Naiman, 1992; Pastor et al., 1993), while it may accelerate turnover rates and speed up succession during early stages (Kielland and Bryant, 1998). Similar indirect effects on nutrient dynamics might also be crucial in understanding the role of moose in the temperate zone.

The present study focuses on how moose might affect nitrogen redistribution in a low-productive fen system in the temperate zone, the Bierbrza National park (Poland). We hypothesize that during spring-summer they forage selectively in sedge-dominated fens (Gębczyńska and Raczyński, 1989), on woody species and a high share of herbaceous species (see for Alaskan moose LeResche and Davis, 1973). Pellets they likely deposit especially at their resting sites at higher forested areas, thus causing a net-export of nutrients away from their feeding sites as has been reported for several species of ungulates (Bokdam and Gleichman, 2000; Moe and Wegge, 2008; Van Uytvanck et al., 2010). We studied whether and how nutrients are redistributed by moose by analysing its diet composition, spatial patterns in foraging intensity and pellet deposition, and nutrient budgets. We discuss the potential role on nutrient dynamics and the effects this may have on willow growth in low-productive fen systems.

2. Methods

2.1. Study area

The study was carried out in the Biebrza National Park in north-eastern Poland. The park covers 200,000 ha, and was established in 1993. The vegetation zonation follows the elevation gradient in a typical sequence: the mineral edge is covered by coniferous forest (*Pinus sylvestris* and *Abies picea*), which turns gradually into a zone of alder forest or alder-birch carr (*Alnus glutinosa, Betula pubescens* and *Frangula alnus*) on peat soils and then into a belt of brushwood (consisting of willow patches, *Salix cinerea*, *Salix pentandra*). These are gradually replaced by open fens with birch shrub and strips of open birch forest (*Betula pubescens*). The floodplain zone closer to the river is dominated by sedge marsh consisting of large sedges (*Carex appropinquata, Carex elata,* and *Carex acuta*) and finally by reed marsh (*Phragmites australis*) along the river bank (Palczynski, 1984). In the Biebrza marshes, moose is the dominant ungulate (no livestock is present in this study area) with an estimated current density of 1- 2 moose km^{-2} (pers. comm. M. Ratkiewicz and Biebrza National Park information). They use the wetland areas mainly as a summer habitat and migrate to the forested areas along the valley edges in winter when their summer habitat is flooded (Gębczyńska and Raczyński, 1989). Red deer and roe deer occur mainly on the higher and drier forest areas in lower numbers. Intermediate sized herbivores as lagomorphs occur in very low density and are virtually absent in the lower parts of the area (pers. observ. D.P.J. Kuijper).

The average annual temperature in the area was 7 °C and the average monthly summer air temperature 18 °C. The annual rainfall was 650 mm. A severe winter with snow cover may last for over 4 months; the vegetation growing season was therefore short, approximately 6 months (April–September).

2.2. Diet analyses and selectivity

Diet composition of moose was determined on the basis of microscopic analysis of epidermal fragments occurring in faecal material. Fresh pellets were randomly collected on transects on which also woody plant species availability was recorded (see below). We took 6–7 pellets from each pellet group that we found. Because dropping density on the transects was low, we additionally collected pellet samples in dense stands of willows and birches in a similar way as described above. In total, 70 pellet samples were collected. Moose pellets were distinguished from red deer and roe deer pellet on the basis of size and shape (Jędrzejewski and Sidorovich, 2010).

Samples of pellets were analysed under a microscope to identify plant species on the basis of epidermal fragments of partly digested plants (according to Kuijper et al., 2009). For this we used a reference collection from plant species from the study area and partly from the near-by Białowieża National Park. We made a mixed sample from small parts of each pellet from one sample. We first crushed large twig fragments, and then grinded the sub-sample to fine dust. This produced cell fragments that were thin enough to be able to see monolayers of cells. A small part was further mixed with 3 ml of tap water and 6 ml of bleach water (39.92 $g L^{-1}$ NaOCl) and soaked for one hour to destroy the chlorophyll and increase the visibility of individual cells. We used the line-intercept method to estimate diet composition (Seber and Pemberton, 1979; Owen, 1975) with the modification that 10 random fragments in the centre of the microscopic field were identified as described by Kuijper et al. (2009). The microscopic slide was analysed in a diagonal way by moving it successive steps of 2 mm up and to the right (for more details see Kuijper et al., 2009). Per mixed pellet sample, 10 microscopic sub-samples were studied. We identified plants into the following categories: woody species; sedges, reed and grasses; herbs; mosses and “unknown”. The veins that could not be assigned to any category because of lack of any specific characteristics, were put into a separate category (“veins”).

We calculated a Jacobs' selectivity index (D) to show whether moose positively ($0 < D < 1$) or negatively ($-1 < D < 0$) select plant species or use them according to their availability ($D = 0$). The index was calculated according to Jacobs (1974):

$$D = (r - p)/(r + p - 2rp)$$

Where, r is the proportion of a species in the diet and p the proportion of a species occurring in the vegetation. The

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