Agriculture, Ecosystems and Environment 222 (2016) 171–184

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures

Anna Oldén[a,*], Kaisa J. Raatikainen[a], Kaisa Tervonen[a], Panu Halme[a,b]

[a] University of Jyvaskyla, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 Jyväskylä, Finland
[b] University of Jyvaskyla, Jyvaskyla University Museum, P.O. Box 35, FI-40014 Jyväskylä, Finland

ARTICLE INFO

Article history:
Received 21 August 2015
Received in revised form 19 January 2016
Accepted 13 February 2016
Available online 22 February 2016

Keywords:
Abandonment
Forest pastures
Pasture-woodland
Semi-natural
Silvopastoral systems
Traditional rural biotopes
Wooded pastures

ABSTRACT

Wood-pastures have been formed by traditional low-intensity livestock grazing in wooded areas. They host high biodiversity values that are now threatened by both management abandonment (ceased grazing) and agricultural intensification, and therefore these habitats are of conservation interest in Europe. In order to explore the effects of grazing on the biodiversity of boreal wood-pastures, we studied the communities of vascular plants and bryophytes in 24 currently grazed and 24 abandoned sites. In addition to the current management situation, we studied the effects of soil pH and moisture, tree density, historical land-use intensity, time since abandonment (in abandoned sites) and grazing intensity (in grazed sites). Grazed sites had higher species richness of both species groups and rare species were also slightly more numerous. Grazing impacted the community composition of vascular plants more than that of bryophytes. For both species groups soil pH (which ranged from 3 to 5) was the most important variable in determining species richness, the number of rare species and the composition of communities. The responses of the two species groups varied somewhat, but generally species richness was maximized on sites with higher soil pH, moisture and grazing intensity, but lower tree cover. We conclude that more effort should be paid on maintaining currently grazed sites under management. If a site has been abandoned, it could be restored into a wood-pasture if it still retains some structural features such as openness and typical species of a wood-pasture. Highest biological conservation values for both management and protection can be found among those sites that are naturally most fertile, but attention should also be paid on the landscape-scale versatility of managed sites.

1. Introduction

Wood-pastures are traditional rural biotopes characterized by long-term systematic grazing of livestock and a varying cover of trees, which can be scattered, located in patches or as a closed canopy. Throughout Europe, different types of wood-pastures have been formed and maintained by traditional low-intensity farming practices (Bergmeier et al., 2010). Wood-pastures host high biodiversity values that are induced by the small-scale heterogeneity of both livestock activities and structural diversity of trees, resulting in small-scale variation in light conditions, microclimate, soil properties, disturbances and various successional stages (Bergmeier et al., 2010; Buttler et al., 2009; Luick, 2009; Olff et al., 1999). Wood-pastures and their biodiversity are threatened by both management abandonment (ceased grazing) and intensification (eutrophication by nutrient accumulation, overgrazing, clearance, regeneration failure, loss of old-growth trees) (Bergmeier et al., 2010). Both abandonment and intensification can result in the decrease of patchiness within a pasture, but also in habitat fragmentation and segregation at landscape-level (Peringer et al., 2013). The abandonment of wood-pastures leads to encroachment of young trees and loss of species that are adapted to semi-open habitats and frequent disturbances (Mariotte et al., 2013; Palo et al., 2013; Paltto et al., 2011; Van Uytvanck and Verheyen, 2014). On the other hand, the climax communities of long-ago abandoned wood-pastures may themselves have high conservation value as they harbor structures (such as old trees and large decaying wood) that are similar to those in old-growth forests (Palo et al., 2013; Paltto et al., 2008).

Large herbivores, including domestic animals, induce fine scale disturbances by removing herbage, trampling and depositing dung and urine (Gillet et al., 2010; Kohler et al., 2004). At the pasture scale these frequent fine scale disturbances create heterogeneity and impact the local processes of species colonization and competitive exclusion (Dufour et al., 2006; Gillet et al., 2010; Kohler et al., 2006a,b; Olff and Ritchie, 1998; Olff et al., 1999). The

* Corresponding author.
E-mail address: anna.m.olden@jyu.fi (A. Oldén).

http://dx.doi.org/10.1016/j.agee.2016.02.018
0167-8809/

effects of grazing on biodiversity can be positive or negative depending on grazing intensity and other site properties. Grazing by natural populations of large mammals or by domesticated animals at low grazing intensity usually increases the diversity of vascular plants, whereas high stocking rates of grazers may have negative impacts on diversity (Belsky, 1992; Milchunas et al., 1988; Pykälä, 2005; Van Wieren, 1995). In addition, other environmental factors such as soil pH, nutrient levels, moisture and light impact the competitive situation between plants and therefore they can have interactions with the impact of grazing intensity. For example, grazers can increase diversity in environments where moisture and nutrients are readily available, but they can decrease diversity if drought or low nutrient levels restrict plant growth (Olff and Ritchie, 1998; Proulx and Mazumder, 1998). Grazers also tend to cause larger changes in species composition in more productive environments (Milchunas and Lauenroth, 1993). Trees improve soil and moisture conditions but also decrease light availability and increase litter accumulation, and as a result, the species richness of field layer plants may be maximized at low to medium tree densities (Gillet et al., 1999). The composition of a plant community, and therefore its response to grazing, is also affected by the site's management history and current and historical habitat connectivity (Bruun et al., 2001; Cousins et al., 2009; Johansson et al., 2008).

The impacts of grazers on bryophytes (mosses and liverworts) are less well known, but grazing has been found to increase bryophyte diversity in several habitat types (Bergamini et al., 2001b; Peintinger and Bergamini, 2006; Takala et al., 2012). However, this is not always the case, especially overgrazing may harm bryophytes as well as vascular plants (Bergamini et al., 2001b). Unlike vascular plants, bryophytes are not grazed by large mammals, but they can be affected by the direct impacts of trampling and dung deposition and by the indirect impacts of herbage removal through decreased competition with vascular plants (Aude and Ejrnæs, 2005; Bergamini et al., 2001b). Many studies have found that a smaller biomass or cover of vascular plants results in higher biomass and diversity of bryophytes, most likely due to decreased competition for light and space and decreased amounts of plant litter (Aude and Ejrnæs, 2005; Bergamini et al., 2001a; Löbel et al., 2006; Takala et al., 2015). On the other hand, the biomass of bryophytes themselves may correlate negatively with their species richness (Ingerpuu et al., 1998). In many cases bryophytes respond to grazing and soil fertility differently than vascular plants and therefore they provide complementary data in the study of grazed habitats (Bergamini et al., 2001b; Takala et al., 2012; Zechmeister et al., 2003). Understanding the effects of grazing on bryophytes is of great importance in habitats such as boreal forests where bryophytes have a large impact on biodiversity and ecosystem functioning (Lindo and Gonzalez, 2010).

The vegetation and biodiversity of boreal wood-pastures have received less research attention than temperate ones. The communities of both vascular plants and bryophytes are a combination of species of forests and open habitats (Schulman et al., 2008; Takala et al., 2015). In Finland a large proportion of forests have historically been grazed by free-ranging domestic cattle during the summers, while a small proportion have been used as fenced semi-open pastures (Jäntti, 1945; Schulman et al., 2008). The currently remaining wood-pastures are all fenced and the tree structure ranges from scattered trees to a closed canopy. Most wood-pastures in the area are densely wooded and they can be called forest pastures (sensu Takala et al., 2015, 2014). In Finland, all types of wood-pastures are threatened habitats due to large declines in their area (more than 99% lost since the 1950s) and quality (eutrophication and intensive forestry practices) (Schulman et al., 2008). Other types of traditional rural biotopes have experienced similar declines and in 2009 only half of the currently remaining Finnish traditional rural biotopes were managed; of these 80% (20,000 ha) were subsidized via the national agri-environment scheme (Kemppainen and Lehtomaa, 2009). Tree encroachment after abandonment of open and semi-open cultural biotopes is the primary threat to 26% of all threatened species in the country (Rassi et al., 2010). In addition to the biodiversity values, multifold social and cultural values are related to these traditional land-use systems (Plieninger et al., 2006).

In order to deepen the understanding of the patterns of biodiversity in boreal wood-pastures, we studied the combined effects of grazing and environmental variables on vascular plant and bryophyte communities by comparing a large number of grazed and abandoned sites with varying environmental properties. The objectives of the study were (1) to determine the effects of current management (grazing vs. abandonment) on the species richness and community composition of vascular plants and bryophytes, (2) to assess how trees, soil properties and historical factors affect the communities relative to the management situation, and (3) to provide recommendations for the management and conservation of different kinds of boreal wood-pasture sites. Based on earlier studies in temperate grasslands and wood-pastures we hypothesized that current grazing increases species richness and changes community composition of both species groups, and more so in sites with high soil moisture and high soil pH. We also expect that the biodiversity of both groups is maximized at low to medium tree densities, medium grazing intensities, high historical land-use intensities, and (in the case of abandoned sites) soon after the abandonment.

2. Materials & methods

2.1. Study sites

Our study sites were located in Central Finland (62°14′N 25°44′E) where the mean annual air temperature is 3–4 °C and precipitation is 600–700 mm year^{-1} (average from 1981 to 2010, Finnish Meteorological Institution, 2015). Out of the 48 study sites, 44 were located on the southern boreal vegetation zone and four close to the border on the middle boreal zone (Fig. 1).

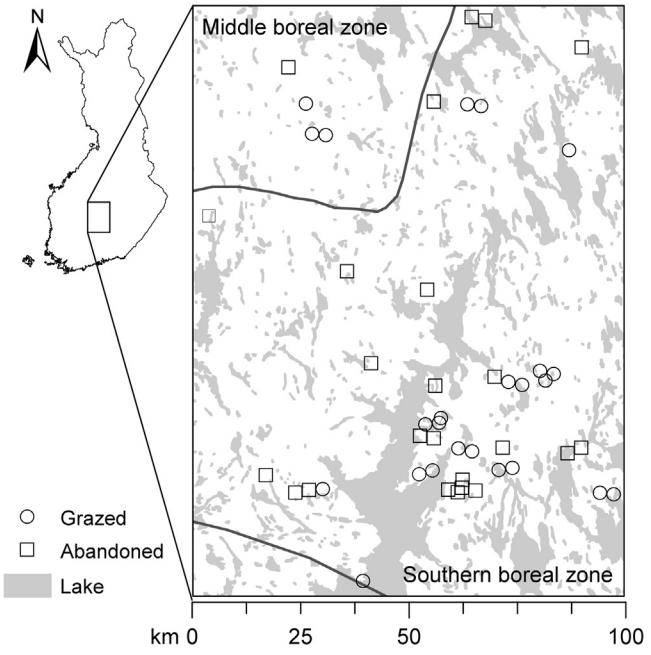

Fig. 1. The location of the study sites in Central Finland. © National Land Survey of Finland 2012.