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Research Paper

Green infrastructure maintenance is more than land cover: Large herbivores limit recruitment of key-stone tree species in Sweden

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ABSTRACT

Due to anthropogenic alteration of stand composition and landscape pattern in Swedish forest landscapes managed for industrial wood production, remnant patches of deciduous forests and woodlands do not form a functional green infrastructure for biodiversity conservation. We assessed if large herbivore browsing hampers the restoration of deciduous forest as green infrastructure by reducing the recruitment of boreal and temperate deciduous tree species of particular importance for biodiversity conservation. A natural experiment approach was applied in the distinct Swedish temperate-boreal forest gradient in Sweden. We measured the potential for saplings of aspen, rowan, sallow and oak to become recruited into the population of ecologically mature trees, as well as the amount of tree and field layer food. Sampling was made in forest stands representing four strata of managed forest landscapes accessible to large herbivores (experiment) and human settlements avoided by large herbivores (control). All four focal deciduous tree species had lower damage levels in controls (towns and villages) compared to experimental (forest) sites. While tree forage was much more abundant in controls, field layer forage in controls was not different from experimental stands. For all tree species except aspen we found a positive relationship between damage levels and large herbivore abundance, to which moose contributed > 89%. We discuss the role of research design for assessing the impact of large herbivores on plants, and highlight the need for integration of multi-species wildlife management as well as conservation planning and management.

1. Introduction

Alteration, fragmentation and loss of habitat all contribute to biodiversity loss. Ecological networks are a solution, and have been subject to research, policy and practice in Europe for decades (; Jongman, Bouwma, Griffioen, Jones-Walters, & Van Doorn, 2011). The EU's Green infrastructure policy (European Commission, 2013) retains this ambition, and aims at maintaining networks of strategically planned representative land cover patches, which are designed and managed to conserve biodiversity, and to deliver a wide range of ecosystem services. The backbone of EU's green infrastructure policy is the Natura 2000 network of high conservation value areas (Salomaa et al., 2017). The EU's Green Infrastructure policy aims at ensuring that conservation, restoration and management of green infrastructure will become part of integrated spatial planning and territorial development. Implementing green infrastructure policy requires maintenance of sufficient amounts of patches of different representative vegetation types, and which form functional ecological networks.

Deciduous forests are one kind of green infrastructure which is critically important for biodiversity conservation in managed forest and woodland landscapes in Europe (e.g., Edman, Angelstam, Mikusinski, Roberge, & Sikora, 2011). However, industrial forestry's focus on conifer wood has led to severe declines of both deciduous forest (e.g., Mikusinski, Angelstam, & Sporrong, 2003; Stighäll, Roberge, Andersson, & Angelstam, 2011) and deciduous woodlands (Myrdal & Morell, 2011; Nilsson, 2006). This is further challenged by intensification of production of goods in forests, woodlands and agricultural land (Andersson, Angelstam, Elbakidze, Axelsson, & Degerman,

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2013; Garrido, Elbakidze, & Angelstam, 2017), and more space being utilised for the expansion of built and transport infrastructure (Sandström, 2002).

Old deciduous trees and forest stands form important habitat components for specialised species in both boreal (Albrectsen et al., 2010; Suominen, Edenius, Ericsson, & de Dios, 2003) and temperate forests (Nilsson, Hedin, & Niklasson, 2001), as well as in anthropogenic wooded grasslands in remnants of once wide-spread cultural landscapes (Bergman et al., 2008; Garrido et al., 2017; Paltto, Thomasson, & Nordén, 2010; Paltto, Nordberg, Nordén, & Snäll, 2011). In the boreal biome this is particularly relevant for the deciduous trees aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and sallow (*Salix caprea*), and in the temperate biome regarding oak (*Quercus robur*), ash (*Fraxinus excelsior*) and lime *(Tilia cordata*). Such deciduous tree species can be termed foundation species (Ellison et al., 2005), and provide key-stone functions in ecosystems.

To ensure that the deciduous forest green infrastructure is functional, there is thus need for both protection and management of existing remnant patches, as well as restoration and re-creation of sufficiently old and ecologically mature deciduous trees and patches as building blocks towards functional deciduous habitat networks (Angelstam et al., 2011; Halme et al., 2013). However, maintenance of green infrastructure is not only about managing the spatial patterns of different land covers, but also managing processes, such as trophic interactions among predators, herbivores and vegetation that affect the opportunity for young deciduous trees to reach ecological maturity and thus serve as habitat for species (Angelstam, Manton, Pedersen, & Elbakidze, 2017). This applies both to old trees and stands in forest landscapes (Andersson et al., 2013; Angelstam et al., 2011), and to so called veteran trees in cultural landscapes (Siitonen & Ranius, 2015).

A key obstacle for restoration of functional deciduous forest and woodland networks is plant-ungulate interactions in terms of the effects large herbivore populations have on vegetation, which extend across both boreal and temperate forests (Augustine & McNaughton, 1998; Hearn, 2015). In Fennoscandia, the young deciduous tree species that are important for biodiversity conservation are also a highly preferred food source for large herbivores such as moose (*Alces alces*) (Bergquist et al., 2014; Bergström & Hjeljord, 1987Bergquist et al., 2014; Bergström & Hjeljord, 1987; Hester, Bergman, Iason, & Moen, 2006; Månsson, Kalen, Kjellander, Andrén, & Smith, 2007), roe deer (*Capreolus capreolus*) (Storms et al., 2008) and red deer (*Cervus elaphus*) (Gill, 2006; Gill & Beardall, 2001; Storms et al., 2008).

Densities of such wild large herbivores have increased over the past decades in Fennoscandia (Côté, Rooney, Tremblay, Dussault, & Waller, 2004). Several studies have shown negative effects of high large herbivore densities on boreal forest biodiversity (Mathisen & Skarpe, 2011; Mathisen, Pedersen, Nilsen, & Skarpe, 2011; Pedersen, 2011; Pedersen, Nilsen, & Andreassen, 2007; Suominen, 1999; Suominen, Danell, & Bergstrom, 1999). Also in the temperate forest biome large herbivores hinder the recruitment of broad-leaved deciduous tree species (Gill, 1992a, 1992b, 2006; Gill & Beardall, 2001; Hothurn & Müller, 2010). Thus, when high densities of large herbivores are maintained, recruitment of focal deciduous tree species for biodiversity conservation into the population of mature and old trees may be hampered (Angelstam, Wikberg, Danilov, Faber, & Nygrén, 2000; Angelstam et al., 2017; Hothorn & Müller, 2010; Myking, Bohler, Austrheim, & Solberg, 2011; Myking et al., 2013). Focusing on the US Yellowstone National Park as a case study Painter, Beschta, Larsen and Ripple (2015) convincingly demonstrated the importance of landscape-scale trophic cascades linked to disappearing and resurgent large carnivore populations' effects on ungulate prey and tree recruitment. Similarly, in eastern North America Nuttle, Royo, Adams and Carson (2013) showed that only low browsing regimes typical of pre-European settlement forests could maintain high tree species diversity.

A key prerequisite for maintenance of green infrastructure is to communicate results from diagnoses of habitat networks' functionality, and factors affecting this, into collaborative land use planning as treatment (Čivić & Jones-Walters, 2014). However, individual countries' and regions' homogeneity in terms predator-prey-vegetation interactions can lead to erroneous conclusions about the role of trophic interactions in green infrastructure planning and management. For example, studies solely within Sweden have concluded that changes in land use practices rather than large herbivore abundance are the important factors for focal deciduous tree recruitment (Bergqvist, Bergström, & Wallgren, 2014; Cassing, Greenberg, & Mikusinski, 2006; Edenius, Ericsson, Kempe, Bergström, & Danell, 2011). However, studies including also neighbouring countries, thus encompassing different large herbivore abundances, clearly demonstrate the opposite result (Angelstam et al., 2000, 2017). A key issue is therefore to design studies within a country or region that can expand the variation in key driving factors so that stakeholder communication about the roles of different factors is enhanced.

The aim of this study is to test the hypothesis that the recruitment of key-stone deciduous tree species is limited by large herbivore abundance at the landscape scale in a gradient between the boreal and temperate forest biomes in Sweden. A natural experiment approach (*sensu* Diamond, 1986) was applied based on the assumption that human settlements (e.g., cities, towns, villages and hamlets) reduce wild large herbivores' access to young forest for feeding (Nikula, Heikkinen, & Helle, 2004), thus reducing browsing damages. We measured browsing damages on young aspen, rowan, sallow and oak trees as an indicator of their potential for recruitment into the populations of old and mature trees in forests (experiment) and settlements (control) along a distinct temperate-boreal forest gradient. We discuss the need for integration of management of trophic interactions on the one hand, and territorial spatial planning to integrate protection, management and restoration of different types of deciduous forest green infrastructure on the other.

2. Methodology

2.1. Study area and study design

Sweden's managed forests range from temperate broad-leaved deciduous to boreal coniferous. To cover this diversity we used the distinct gradient from the northernmost occurrence of temperate broad-leaved deciduous tree species such as oak to the southernmost part of the boreal biome in south-central Sweden (Malmgren, 1982), and thus chose a 44,560 km^2 large study area at ca. 58.5°–60.5° northern latitude (Fig. 1). This gradient is characterised by a transition from forest landscapes with a long land use history with temperate forest tree species in the south to a boreal forested landscape with a short land use history in the north (Angelstam et al., 2015). Altitude increases from 2 m above sea level (m a.s.l.) in the south to 561 m a.s.l. in the north. The southern part of the study area is dominated by agricultural land < 30 m a.s.l. with islands of temperate forest managed by private land owners. Forests dominate areas > 30 m a.s.l., and are owned by large industrial forest companies or non-industrial private forest owners.

The spatial extent of trophic interactions between large mammalian carnivores and large herbivores and vegetation, as well as subsequent cascading effects in forest landscapes, limits the application of replicated experiments. An alternative option is natural experiments (*sensu* Diamond, 1986) in the form of comparative macro-ecological studies that trade off the precision of small-scale research with an appropriate spatial scale (Brown, 1995). To assess the impact of large herbivores on boreal and temperate deciduous tree species of special importance for biodiversity conservation we designed a stratified random sampling procedure within (1) sampling sites providing full access to large herbivores in rural forest areas (experiment) and (2) sites located within settlements ranging from towns to villages and hamlets