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Long-term effects of wild ungulates on the structure, composition and succession of temperate forests

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ABSTRACT

Ungulates in temperate regions are increasing in range and abundance, leading to concerns that browsing and trampling reach levels that hamper tree recruitment and forest regeneration. However, studies that actually quantify the long-term effects of ungulates on forest succession are scarce. Here, we use a chronosequence of ungulate exclosures (fenced) and control (unfenced) plots to assess the long-term effects of ungulates on forest structure, diversity and litter depth in forests on poor sandy soils at the Veluwe, the Netherlands, which have moderate ungulate densities ($\bar{x}$ = 13.6 ungulates km^{-2}). We surveyed the vegetation in 27 paired fenced and unfenced plots that ranged from 1 to 33 years old, and measured seven variables to characterize forest structure (stem density, canopy cover and understory vegetation cover), composition (Shannon diversity, species richness and conifer proportion) and leaf litter depth. We found on average that fencing compared to unfencing reduced understory vegetation cover (fenced = 64.3 ± 20.2%, unfenced = 80.3 ± 19.4%), increased canopy cover (fenced = 47.4 ± 30.1%, unfenced = 29.3 ± 21.1%), tree species richness (fenced = 4.5 ± 1.3 spp., unfenced = 2.7 ± 1.2 spp.), tree Shannon diversity (fenced = 1.1 ± 0.3 index, unfenced = 0.7 ± 0.3 index) and litter layer depth (fenced = 4.4 ± 1.4 cm, unfenced = 2.4 ± 1.1 cm). While fenced plots developed woody vegetation with palatable broadleaved species such as *Betula pendula, Betula pubescens, Prunus serotina,* and *Quercus robur*, unfenced plots were not associated with any particular tree species. Our results show that current ungulate densities in this system have pronounced long-term effects on forest structure, composition and litter depth, implying that ungulates can slow down natural succession of temperate forest, from light demanding to shade tolerant species, by keeping the system in an arrested state consisting of light demanding species.

1. Introduction

Wild ungulates are expanding in temperate forests and have reached historical peaks in abundance during the last decades (Clutton-Brock & Albon, 1992; Rooney, 2001; Pellerin et al., 2010) due to a variety of reasons including reintroduction, reduced competition with domestic cattle, abandonment of agricultural pastures that induce woody species encroachment which favour preferential habitat type for ungulate species, reduced hunting levels and absence of top predators (Kuiters et al., 1996; Rooney, 2001). Ungulates are keystone species and ecosystem engineers (Power et al., 1996; Waller & Alverson, 1997; Rooney, 2001) because through browsing they shape the structure and dynamics of entire ecosystems, from the micro scale (e.g., tree diversity in the forest stand) up to the landscape scale (e.g., open understory on a regional forest) (Russell et al., 2001; Rooney & Waller, 2003). Ungulates can modify vegetation and steer succession through a variety of mechanisms, such as herbivory (browsing, grazing), disturbance (trampling, fraying, uprooting), and nutrient translocation (defecation) (Reimoser, 2003).

Ungulates may steer forest composition in two major ways. The first is preferential browsing and grazing of more palatable species such as broadleaved tree species, which indirectly favours less palatable species

Abbreviations: PCA, Principal Component Analysis; GLMM, Generalized Linear Mixed Models

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such as most conifers (Rooney & Waller, 2003). This preference may cause a shift from mixed broadleaved-conifer forests to conifer-dominated forests in temperate regions (Gill, 1992; White, 2012), and may facilitate the establishment of less palatable invasive species through competitive release and increased resource availability (Kalisz et al., 2014). Second, frequent and intense physical disturbance such as trampling, fraying and uprooting can eliminate entire cohorts of seedlings and saplings from a forest stand (Gill, 1992). Such damage to recruits in the forest understory may slow down forest succession and may eventually lead to forest collapse if there are no young trees to replace senescent adult trees (Côté et al., 2004). Thus, ungulates may determine the boundaries between open and closed vegetation between biomes (e.g., modifying the transition from forest to savannah) as well as within biomes (e.g., modifying the transition between open and closed forest patches).

In northwest European forests, ecological succession normally proceeds from an early-successional vegetation dominated by light-demanding *Betula*, *Pinus* and *Quercus* species towards a late-successional vegetation dominated by shade-tolerant species such as *Fagus sylvatica* (Zerbe, 2002). However, when ungulates are present at high densities, browsing may reduce tree density and shift species composition towards an arrested, early-successional vegetation, dominated by light-demanding pine species (Kuiters & Slim, 2002). These shifts in species composition may also have cascading effects on other trophic levels, such as a reduced number of invertebrate decomposers resulting in reduced litter decomposition, and a decreased diversity of small mammals that need heterogenous forest structure as shelter from weather and predation (Fuller, 2001; Chollet et al., 2015).

The short-term effects (e.g. < 5 years) of ungulates on forest regeneration have been widely documented. At low densities and on relatively fertile soils, ungulates can promote structural heterogeneity (Gordon & Prins, 2008; Prins & Fritz, 2008; Svenning et al., 2015) leading to an increase in herbaceous and woody plants, higher animal diversity (invertebrates and vertebrates) and improved ecosystem functioning such as transfer of energy up the food chain (Kuiters et al., 1996; Gill & Morgan, 2010; Estes et al., 2011). However, it is not clear how the effects of ungulates play out on the longer-term (e.g. > 15 years) (Scott et al., 2009); as ungulates in the short-term tend to browse mainly on palatable (broadleaved) species such as *Sorbus aucuparia* and *Betula pendula*, leading to a competitive release of unpalatable (coniferous) species such as *Pinus sylvestris* and *Picea abies* that are hardly browsed. The potential long-term effect of ungulates is difficult to evaluate due to the lack of long-term and replicated experiments (White, 2012).

Here, we aimed to assess the long-term effects of a relative moderate ungulate density on forest structure, diversity and functioning under relatively poor nutrient conditions at the Veluwe, the Netherlands (Kuiters & Slim, 2002). We applied a chronosequence approach that uses a space-for-time substitution to infer long-term successional trends (Kennard, 2002). Specifically, we surveyed 27 pairs of fenced and unfenced plots, ranging in age from 1 to 33 years old, at 17 sites. We asked what the long-term effects of ungulates are on forest structure, composition and succession.

We tested four predictions: (1) ungulates reduce stem density, understory vegetation and canopy cover through browsing and trampling (Gill & Beardall, 2001; Russell et al., 2001), with an accumulating impact over time. (2) Ungulates reduce seedling and sapling richness and diversity by selectively browsing on broadleaved trees, and favour conifers through competitive release (Côté et al., 2004). (3) Ungulates can either reduce or increase the depth of litter and fragmented layers. Ungulates can reduce litter thickness by removing litter, or by compacting litter through trampling. Ungulates can also change litter thickness by preferentially feeding (Husheer et al., 2005) on broadleaved species, which leads to a stand dominated by coniferous species. Conifer stands may either have a thin litter layer because of their evergreen leaf habit, which is associated with low annual litter production rate. Alternatively, conifer stands may have a thicker litter layer because of the low decomposability of their needles, and their irregular packing. The relative importance of these two processes determine in the end the depth of the litter layer. (4) In the absence of ungulates, succession proceeds from stands dominated by light-demanding species towards stands dominated by shade-tolerant species. Active browsing by ungulates on palatable species leads towards an arrested, early-successional vegetation, dominated by light-demanding conifer species in the forest understory (Kuiters & Slim, 2002).

2. Methods

2.1. Study area

The Veluwe is located in the central part of the Netherlands with a total extension of $1200\,km^2$. Annual average precipitation is $900\,mm\,yr^{-1}$, whereas the annual average temperature is 9.4 °C, with monthly temperature means ranging from 2.5 °C in January to 16.4 °C in July (Kuiters & Slim, 2002). The main soil types consist of xeric humic podzols and brown earths (inceptisols), depending on the parent material that range from aeolic drift and cover sands to Pleistocene loamy fluvioglacial sands (Kuiters & Slim, 2002). The Veluwe is covered by a mosaic of forests, drift sands and heathland, where forests cover two thirds of the total area. The main species are *Pinus sylvestris, Quercus robur, Fagus sylvatica, Larix kaempferi, Pseudotsuga menziesii* and *Betula pendula*. Although ungulate assemblage varies across the Veluwe, the main species are roe deer (*Capreolus capreolus),* fallow deer *(Dama dama),* red deer *(Cervus elaphus)* and wild boar *(Sus scrofa),* with an average density of 13.6 animals per km^{-2} in 1998 (Kuiters & Slim, 2002) and considerable increase during the last decades. Forest managers in this area generally aim to transform even-aged single coniferous species into mixed forest stands, and create small clearings to stimulate natural regeneration of a mix of native species.

2.2. Study design

To assess the effects of wild ungulates on long-term forest succession, we compiled a set of existing fenced plots that were established in recent clear cuts to protect forest regeneration from ungulates, paired with neighbouring unfenced plots, that were ca. 10 m apart. In total, we identified 27 fenced and unfenced plots in 17 different forest sites with plots ranging in age from 1 to 33 years since establishment. Plot size varied from 0.01 to 0.75 ha, and the number of pairs per site varied from 1 to 6 (Appendix A.1). We surveyed the vegetation during the late summer of 2016 and 2017. Within each pair of fenced/unfenced plots, 5×5 m quadrates were randomly established by drawing numbers for the x and y axis, which represented a coordinate system. We established two quadrates per plot when regeneration heterogeneity was low (i.e., low species diversity and little variation in forest structure), and three or four quadrates per plot when heterogeneity was high. Data from all quadrates were averaged to obtain values for a plot.