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Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review

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ABSTRACT

Wild ungulates such as red deer, roe deer and wild boar are key drivers of forest ecosystems. Across the northern hemisphere, their range and abundance is increasing, while at the same time forest conversion and habitat fragmentation have led to a large variation in ungulate density and composition among areas. Understanding ungulate density impacts are important in order to prevent shifts towards undesired states, such as from forest to heathland. Here, we assess the effects of ungulate density on forest regeneration, development and functioning. We carried out a systematic literature review of 433 published studies in temperate forests, and used the data to model dose-response curves of the effects of ungulate density on three sets of forest attributes; tree regeneration (abundance, species richness and composition), forest structure (horizontal and vertical), and forest functioning (nutrient cycling in soil, timber and food production). Ungulate density averaged 23.6 km^{-2} across studies. Ungulates had a negative effect on forest regeneration, structure and functioning in 70% of the evaluated cases. The dose-response curves had a sigmoidal, rather than a unimodal shape. Critical tipping points, where ungulates started to have a negative effect on forest regeneration, were found at an ungulate metabolic weight density of 115 kg km^{-2} for forest regeneration, 141 kg km^{-2} for forest structure, and 251 kg km^{-2} for forest functioning, which is roughly equivalent to 10, 13 and 23 roe deer per km^{-2}. Forest regeneration was most sensitive to immediate browsing and trampling impacts of small seedlings, while forest functioning was least sensitive because of time lags. However, these effects may build up over time. We suggest research priorities for studying ungulate-plant interactions in temperate forests, and make management recommendations how to balance wildlife with a functioning forest.

1. Introduction

Wild ungulates are increasing in density across the northern hemisphere (Glutton-Brock and Albon, 1992; Reimoser, 2003; Pellerin et al., 2010) because of ungulate reintroduction, abandonment of agricultural land, competitive release from domestic ungulates, absence of top predators, stricter hunting regulations and improvement of habitat quality (Kuiters et al., 1996; Rooney, 2001; Côté et al., 2004). Apart from inter-annual fluctuation, habitat quality and predation, conversion of natural forests to managed forests (Gordon and Prins, 2008) has led to the isolation of ungulates in different forest fragments (Kuiters et al., 1996). This has resulted in a large variation in ungulate density between fragments, and hence, a large variation in ungulate effects on the environment. Many temperate forests currently harbour large ungulate populations resulting in intensive plant-animal interactions. Whether these population levels are acceptable is the subject of intensive debate among stakeholders (Horsley et al., 2003).

Ungulates affect ecosystems through browsing, trampling, fraying, stripping, uprooting, defecation and seed dispersal (Bruinderink and Hazebroek, 1996; Reimoser, 2003; Pellerin et al., 2010). These interactions are key determinants of the structure and dynamics of woody ecosystems. For instance, when ungulates are regulated naturally by predation and intraspecific competition, large herbivores can remove up to 10% of the above ground bottom-up control, where plants limit ungulate populations by chemical and structural defences that prevent herbivory, and top-down control, where predators regulate ungulates by predation (Terborgh et al., 2001).

Ungulates affect ecosystems at different organizational, spatial, and

Abbreviations: MWD, metabolic weight density

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temporal scales, ranging from the local patch up to the landscape scale. For instance, removal of the vegetation biomass has implications for local plant composition and structure, and with time this may lead to changes in soil fertility and the landscape, thus affecting the entire food web (Gordon and Prins, 2008; Prins and Fritz, 2008; Svenning et al., 2015). Their effect can enhance or reduce natural processes and patterns; which may directly affect species regeneration, forest structure and ecosystem functioning (Reimoser, 2003).

Whether ungulates have a positive or negative impact on ecosystems depends on their density, browsing intensity, local biotic and abiotic conditions, and forest management (Van Hees et al., 1996; Heckel et al., 2010; Pellerin et al., 2010). Because of their important role in ecosystem functioning, ungulates are considered to be keystone species and landscape modifiers (Rooney, 2001). Hence understanding the relationship between ungulate abundance and forest regeneration is fundamental.

Whether ungulates have positive, neutral, or negative effects on forest attributes depends on the shape of the dose-response curve and lag times (Nuttle et al., 2014). The most plausible shape of this dose-response curve is unimodal (Rooney and Waller, 2003). At low ungulate density, forests have a low plant species diversity because of a structurally uniform and dense vegetation with little heterogeneity in light and habitats. At intermediate ungulate density, forests have higher habitat heterogeneity due to vegetation removal, seed bed preparation (by litter removal and soil disturbance), and seed dispersal (Lucas et al., 2013). At the same time, ungulates may steer plant competition and succession through selective browsing on palatable species, thus facilitating the establishment of other plant species (Kuiters et al., 1996; Fuller and Gill, 2001; Brullhardt et al., 2015). Furthermore, as a result from low ungulate trampling, soil compaction is low and thus facilitating seedling establishment. At high ungulate density, however, tree regeneration is hampered by over-browsing, while selective browsing may lead to suppression of palatable species thus reducing tree species diversity (Tyler et al., 2008; Schippers et al., 2014). In ecotone transitions, it is even possible that forest shifts towards an alternative stable grassland state (Côté et al., 2004), with a high degree of soil compaction, low stem density and almost no canopy cover.

Understanding ungulate density impacts are important in order to prevent shifts towards undesired states, such as from forest to heathland (Scheffer et al., 2001; Folke et al., 2004). However, despite a wealth of studies that have assessed the effect of ungulates on vegetation, we know very little about the shape of the dose response curve between ungulate density and forest attributes, and whether there are critical thresholds and tipping points (Putman et al., 2011; Reimoser and Putman, 2011).

Here, we aim to (1) provide a synthetic review on the effects of ungulate density on the regeneration, structure and functioning of temperate forests, from both northern and southern hemispheres, (2) quantify the dose-response relationships between ungulate densities and forest attributes, and (3) identify potential thresholds and tipping points for each dose-response. Our study provides a first average global estimate of what ungulate densities may be critical for forest development in temperate zone. We then discuss ungulate management strategies and identify research priorities for animal-plant interactions in temperate forests.

2. Methods

We searched three literature data bases (CAB Abstract, Web of Science and Scopus) for scientific publications on the effects of wild ungulates on temperate deciduous forests. Although ungulate species are currently increasing in range and density especially in Central Europe and North America, ungulate species from other continents were included as well to have a wider overview. We used the following combination of keywords: “(mammals or mammal or mammalia or deer or mouflon or wild boar) and (forest or trees or forests) and (seed dispersal or browsing or trampling or stripping or defecating or rooting or fraying) and (structure or species richness or abundance or functioning) and (temperate or seasonal or deciduous)”. We retrieved 469 articles, from which 164 studies were utilized for our analysis because they yielded information on the study region, ungulate species, ungulate abundance and effects on different forest response variables. All extracted information was organized in an Excel file by response variable. For each reported case, corresponding information on the type of effect, ungulate species, ungulate abundance/density and research area was incorporated.

2.1. Forest responses

All response effects were than grouped into three broad response attributes, each consisting of 2–3 similar forest components. This was done in order to have enough data points and statistical power for the analysis. The three forest response attributes consist of forest regeneration (i.e., the amount, diversity, and seedlings and saplings composition), forest structure (i.e., horizontal patch structure and vertical forest layering), and forest functioning (i.e., nutrient cycling in soil, tree growth and provision of wild forest food). Because studies differed widely in the temporal scale, survey design, environmental conditions, response variables used and measurements procedures, we quantified ungulate effects in a qualitative way mainly to enhance comparability across a large array of heterogenous studies. For each response variable, it was evaluated whether ungulate presence or density had a significantly positive (1), significantly negative (−1), or no significant effect (0). In total, we compiled 435 cases.

2.2. Ungulate density

For each study, the ungulate species and density were recorded. To be able to assess the combined effects of different species, ungulate density was expressed as metabolic weight density (MWD) using the following formula: $MWD = mass^{0.75}$ (Kleiber, 1947). This allowed the standardization of ungulate density based on their nutritional needs. A standard body mass (in kg) was used for the different ungulates species (Table 1). If a mix of ungulates was presented without identification we used 96 kg as an average for the most common *cervidae* species presented across the studies.

Table 1
Ungulate standard weight and representation of ungulate species from total number of reported species.

Common name	Species	Weight (kg)	%	Source
Buffalo	*Bison bison*	650	1,1	Lott and Galland (1987)
Moose	*Alces alces*	425	3,6	Stephenson et al. (1998)
Elk	*Cervus canadensis*	250	1,9	Cook et al. (2003)
Red deer	*Cervus elaphus*	190	11,2	Gill and Morgan (2010)
Sika deer	*Cervus nippon*	110	5,8	Suzuki et al. (2001)
Wild boar	*Sus scrofa*	80	9,4	Genov and Massei (2004)
Fallow deer	*Dama dama*	65	2,8	Gill and Morgan (2010)
White-tailed deer	*Odocoileus virginianus*	60	28,3	Hefley et al. (2013)
Chamois	*Rupicapra rupicapra*	35	1,1	Garcia-Gonzalez and Cuartas (1996)
Roe deer	Capreolus capreolus	25	7,1	De Jong et al. (1995)
Black-tailed deer	*Muntiacus reevesi*	18	2,6	Parker et al. (1993)
Pudu	*Pudu pudu*	12	1,1	Merino et al. (2005)
Ungulates	Mix of species	96	24	