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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 | |

### 2.3. Statistical analysis

We compared the relative frequency of response types (positive, neutral or negative) for each forest component with Chi-square tests. We used Multinomial Logistic Regression analysis to fit dose-response curves, in which ungulate density was expressed in terms of MWD, and ungulate effects were classified as being significantly positive (1), not significant (0) or significantly negative (−1). All model assumptions are met, such as: an independent continuous variable, a nominal continuous variable, independent observation, low multicollinearity and large sample size. The independent variable, MWD, was transformed to $\log_{10}$. These models have a sigmoid shape. To allow for unimodal responses to ungulate density, we evaluated whether adding the square of ungulate density significantly improved the model (Augustin et al., 2001; Merino et al., 2005). Dose-response curves were fitted for all three forest attribute responses (forest regeneration, forest structure and forest functioning) to increase power and obtain generalities, as well as for each of the individual 8 response variables to obtain more detailed insight. For each analysis, we calculated $\text{Chi}^2$, the coefficient of determination, the probability value and the degrees of freedoms of the model. To identify critical ungulate densities that reflect tipping points in forest response, we quantified at what value of ungulate density the average response value as fitted by the curve became greater than 0.5 (from neutral to positive) or smaller than −0.5 (from neutral to negative).

## 3. Results

### 3.1. Ungulate effects on forest regeneration, structure, and functioning

From the total of 435 cases compiled, 50.5% were situated in North America, 31.9% in Europe, 7.2% in Oceania, 6.8% in Asia and 3.6% in South America. Ungulates had a significantly negative effect on forest attributes on most (70%) of the cases. In 11% of the cases a significantly positive effect was reported, ranging from food production with 0% to horizontal structure with 22% (Fig. 1). In 19% of the cases no effect was detected.

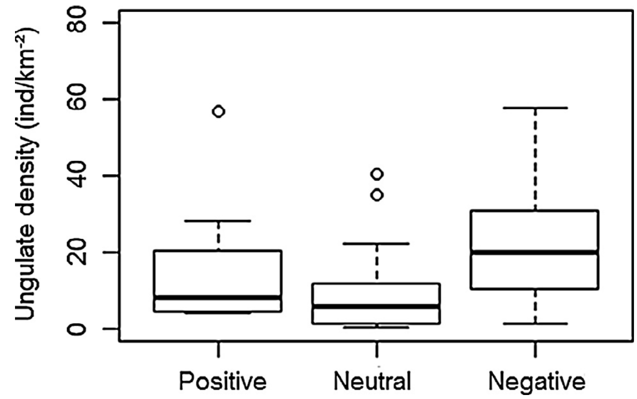


**Fig. 2.** Positive, negative and neutral effects of wild ungulates on different forest attributes are associated with different ungulate densities (Kruskal-Wallis test, Chi square = 16.78, $P < 0.001$). The reported number of cases are 20 for positive, 39 for neutral and 162 for negative. Boxplots of ungulate densities are shown and their significance test; positive vs. neutral $P = 0.081$, positive vs. negative $P < 0.000$, neutral vs. negative $P < 0.000$ (pairwise-Mann-Whitney *U* test). Horizontal "line" indicates the median. The "box" represents the middle 50% of scores for the group. The upper and lower "whiskers" represent scores outside the middle 50%. Outliers are plotted as individual "points".

Negative effects of ungulates were most frequently reported for wild food provision (in 100% of 8 cases), on regeneration abundance (in 79% of 139 cases) and forest composition (in 78% of 108 cases). Positive effects were most frequently reported for horizontal forest structure (in 22% of 45 cases) and on nutrient cycling in soil (in 21% of 29 cases). Finally, ungulates had most often non-significant effects on timber production (in 31% of the cases) and nutrient cycling in soil (in 35% of the cases).

Ungulate densities varied from < 1 to > 300 $\text{km}^{-2}$ across studies. Average ungulate density was greater for studies that reported a negative effect on forest attributes (on average 28 $\text{km}^{-2}$), than for studies

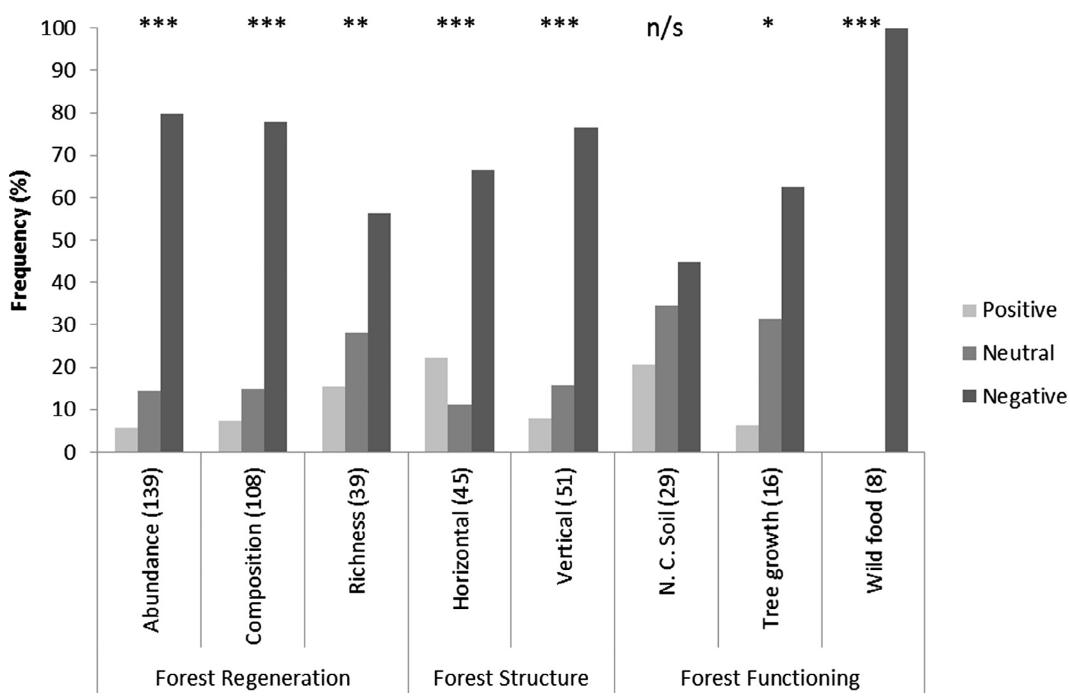


**Fig. 1.** Relative frequency of ungulate effects (significantly positive, neutral, or significantly negative) on forest regeneration (abundance, composition and richness), forest structure (horizontal and vertical) and forest functioning (nutrient cycling in soil and the provision of food and timber). The sample size is given in parentheses. Significant differences in the relative frequency of response types (positive, neutral or negative) within a forest component are tested with a Chi-square test (d.f. = 2) and indicated by asterisks. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ and n.s. $P > 0.05$.

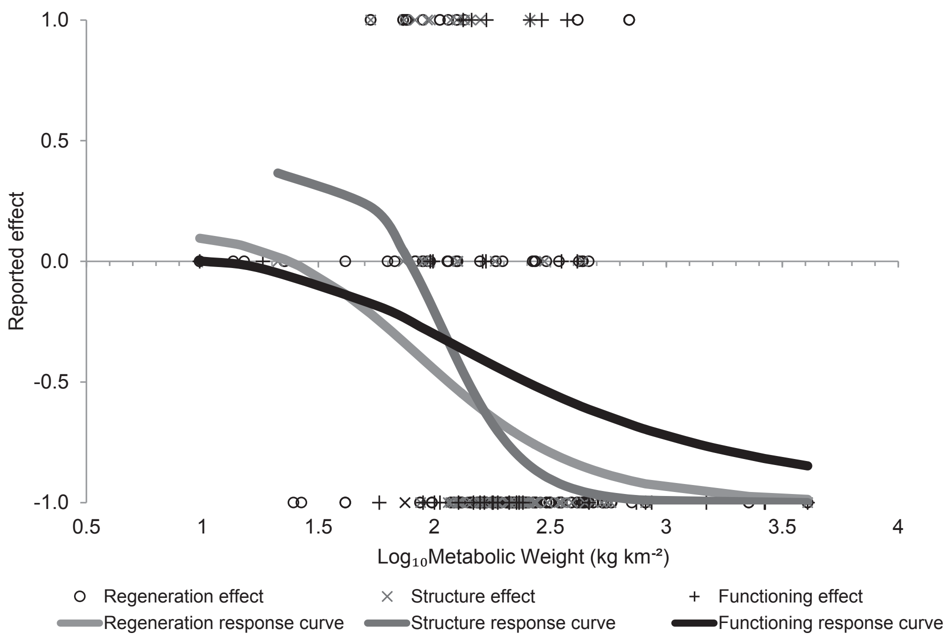


**Fig. 3.** Dose-response relationship between Metabolic Weight Density and the probability of studies reporting a significantly negative (−1), neutral (0) or significantly positive (1) effect on each forest attribute – Forest regeneration (N = 221 cases), forest structure (N = 84), forest functioning (N = 42) – summarized with multinomial logistic regression curves. Each of the forest attributes are shown with different shades of grey and different symbols.

that reported positive or neutral effects on the different forest attributes (on average 15 $km^{-2}$ and 11 $km^{-2}$ respectively) (Fig. 2).

### 3.2. Dose-response relationships

The dose-response curves (Fig. 3, Appendix A1) reported effects on forest attributes, which were more negative as ungulate abundance increased. This was the case for forest regeneration (Multinomial logistic regression, $X^2 = 36.80$, $R^2 = 0.20$, $P < 0.001$, df = 2, Fig. 3), forest structure ($X^2 = 24.88$, $R^2 = 0.33$, $P < 0.001$, df = 2 Fig. 3), as well as forest functioning ($X^2 = 7.84$, $R^2 = 0.22$, $P = 0.02$, df = 2 Fig. 3). The dose-response curves were generally sigmoidal declining, and no unimodal curves were found. The thresholds, where ungulates tended to switch from generally neutral effects towards significantly negative effects was observed at a value of −0.5. The threshold was lowest ($Log_{10}2.06$, or 115 kg of metabolic weight $km^{-2}$) for forest regeneration, the threshold occurred at intermediate ungulate density ($Log_{10}2.15$ or 141 kg $km^{-2}$) for forest structure and the threshold occurred at highest ungulate densities ($Log_{10}2.40$ or 251 kg $km^{-2}$) in the case of forest functioning. Across the evaluated studies, the average MWD was $Log_{10}2.306$ or 202 kg $km^{-2}$.

## 4. Discussion

How ungulates affect temperate forests is a major concern of forest and nature managers, especially in regions where ungulates are increasing in abundance (Pellerin et al., 2010). This study is the first semi-quantitative review on the effects of ungulate abundance on temperate forests at a global scale. Dose-response curves that we fitted to link reported effects of ungulates to ungulate density revealed that effects on a variety of forest characteristics changed from neutral to generally negative as ungulate density increased. There was no optimum density for a positive effect on forests, but rather a gradual decline with an increasing density, followed by a steep decline (inverted sigmoidal curve). As ungulate density increases, there is a rapid shift from neutral to negative effects on the regeneration, structure and functioning of forests around a MWD of 169 kg $km^{-2}$, which is equivalent to 15 roe deer per $km^2$ or 8 white-tailed deer per $km^2$.

### 4.1. Ungulate effects on forests

Negative effects were clearly more frequent than positive and neutral effects (Fig. 1). From all response variables, ungulates had the strongest negative effect on food production (in 100% of the cases), although the sample is too small (N = 8) to draw strong conclusions. Regeneration abundance and forest composition decreased in 79% and 78% of the cases, as selective browsing reduced the abundance of palatable species and increased the abundance of less palatable species through competitive release (Schippers et al., 2014).

Ungulates had the strongest positive effect on horizontal forest structure (in 22% of the cases). This is explained by the fact that ungulates create horizontal heterogeneity by generating open areas by vegetation removal and by dispersing seeds, thus promoting tree species distribution across the forest (Eycott et al., 2007). Nutrient cycling in soil increased (in 21% of the cases), as ungulates increase nutrient availability and heterogeneity through defecation and litter removal from the forest floor (Murray et al., 2014).

Ungulates had most often neutral, i.e., non-significant effects on timber production (31% of the cases) and nutrient cycling in soil (in 35% of the cases), probably because a larger time span (> 50 years) is needed for ungulates to affect wood production (Welch and Scott, 1998) and the entire trophic levels in order to change local soil conditions.

### 4.2. Thresholds: Ungulate densities

Our results indicate that ungulates negatively affect regeneration in temperate forests beyond densities of 115 kg $km^{-2}$ (MWD), which is equivalent to 2.3 red deer, 4.3 wild boar, 5.3 white-tailed deer or 10.2 roe deer per $km^2$. The high apparent sensitivity of regeneration to ungulates is probably because seedlings and saplings are relatively vulnerable to intermediate browsing and trampling, and because seedlings and saplings are highly dynamic and respond rapidly to environmental change. Our results are similar to the threshold density of 4 red deer suggested in a Scottish forest study (Putman et al., 2011), but below the suggested threshold density of 14 deer per $km^2$ for a mix of deer species (roe, muntjac and fallow deer) in a lowland UK forest (Gill and Morgan, 2010). This variation can be explained by a combination of primary productivity and ungulate composition. Our estimates are not representative for one particular area, but represent the general pattern across all temperate forests globally.

We found that ungulates negatively affect forest structure beyond a MWD of 141 kg $km^{-2}$, which is equivalent to 2.7 red deer, 5.2 wild boar, 6.5 white-tailed deer or 12.5 roe deer. The fact that the threshold is higher than forest regeneration reflects that stem density and development of less palatable species is relatively insensitive to ungulates. Our estimates are similar to stem density thresholds reported in earlier studies, e.g., 8 white-tailed deer per $km^2$ in a Pennsylvanian forest (Horsley et al., 2003) and 4–8 white-tailed deer in a Wisconsin forest (Alverson et al., 1988).

Finally, forest functioning was negatively affected beyond a MWD of 251 kg $km^{-2}$, which is equivalent to 4.9 red deer, 9.4 wild boar, 11.6 white-tailed deer or 22.5 roe deer. The threshold is again higher for forest functioning, probably because browsing limits regeneration growth and reproduction. These threshold estimates are similar to 4 red deer per $km^2$ in a British forest (Holloway, 1967) and 7–15 white-tailed deer per $km^2$ in a Pennsylvanian forest (Tilghman, 1989), but much higher than 4–12 roe deer reported in a British commercial forest (Reimoser and Putman, 2011). This variation can be explained by different methods used to estimate ungulate density and their effect on vegetation, as well as other factors that mediate these interactions such as primary productivity. For example, more fertile soils and higher primary productivity allow for higher ungulate densities (Cromsigt and Kuijper, 2011).

Our multinomial logistical regression analysis was only based on whether a significant ungulate effect (positive or negative) was detected in the original studies, and not based on effect sizes. This allowed us to include a greater number of studies with a variety of methodologies. Future research could study effect sizes, to get a more precise estimate of ungulate impacts.

Although our data came from temperate forest studies from all continents, most cases (82%) came from North American and European forests, reflecting the common bias in research efforts. Similarly, due to our search criteria, we recognise that our study has bias towards deer species, relegating other wild ungulate species, such as: moose and elk.

We acknowledge that not all temperate forests respond equally to different ungulates densities and composition, hence that a single dose-response relationship cannot represent the reality of all temperate deciduous forests. We used metabolic weight density rather than absolute density, taking the metabolic properties of these different species into account. We acknowledge that such an approach is still not perfect because ungulate species also have different behaviour, that is not entirely explained by their metabolic weight. The tipping points we have identified are likely to be higher in more fertile systems, and lower in more infertile systems (Cromsigt and Kuijper, 2011).

### 4.3. Managing ungulate effects on forests; towards an optimal ungulate density

Our results suggest that switching from negative to neutral or even positive ungulate effects it is necessary to reduce ungulate densities, at least temporarily. Such a release of plants from natural enemies provides a time window of opportunity for tree regeneration (Nuttle et al., 2014). Once saplings attain a minimum size (e.g., 1.6 or 2.0 m in height, depending on the particular ungulate assemblage) they can escape herbivore pressure, because their top shoot is out of ungulate reach, and because plants are sufficiently robust to recover from herbivory (Motta, 2003; Renaud et al., 2003) and fraying. The time window needed for forest recovery depends on seed availability and tree species growth rate. Hence, for lowland central Europe it will be relatively short (i.e., 3 years) for fast-growing light-demanding species (e.g., *Betula pendula* and *Pinus sylvestris*), the time window of recovery will be relatively long (i.e., 10 years) for slow-growing and palatable species (*Quercus robur*, *Quercus petrea*, and *Tilia cordata)*. Whereas if the system experiences neutral or even positive effects from ungulates, it is expected that the three main plant defence mechanisms (resistance, tolerance and escape) are enough to secure their establishment and reproduction (Lindroth and St. Clair, 2013).

Forest managers and stakeholders can enhance forest heterogeneity at different spatiotemporal scales by rotating ungulate exclosures at different frequencies (e.g., 3–10 years) and sizes (e.g., 0.1–1 ha) (Augustine and Frelich, 1998), by offering alternative foliage for ungulates, changing landscape structure such as shelter provision or even by modifying the forest edge (Reimoser and Putman, 2011). Forest managers can also steer the landscape of fear by reintroducing top predators (Sergio et al., 2008), varying hunting pressure over space and time (Cromsigt et al., 2013), or managing ungulate sex ratio within a population, for instance limiting the number of reproducing females (Clutton-Brock et al., 2004).

Rewilding natural areas with apex predators, might bring ungulates density into balance again and thus secure regeneration establishment and development. Predators can eventually restore top-down interactions and associated cascading effects that culling and game hunting have failed to achieve. On natural areas trophic rewilding gives the opportunity of self-regulation, thus providing new opportunities for the entire ecological community and reducing human interference (Svenning et al., 2015).

### 4.4. Research priorities and outlook

We used qualitative data to characterize the responses from a wide variety of temperate forests and showed a non-linear relationship between ungulate density and forest regeneration (Gill and Morgan, 2010). However, the coefficient of determination was rather low, indicating a high variability among independent and dependent variables. To better understand how ungulate density affects forest development, the dose-response curves should be produced more accurately. Our study is a first important step based on data from literature review, but results were combined from studies in many different forest systems, which used different methods to quantify ungulate densities and forest responses. Modern techniques, such as surveys with camera traps, can provide more accurate and more standardized ungulate density estimates, detecting animals with a wide range in body sizes and different levels of shyness, 24 hrs per day (Rowcliffe et al., 2011).

## 5. Conclusions

Understanding effects of wild ungulates is essential to the management and conservation of temperate forests. Much of the recent debate on ungulate management has focused on the carrying capacity of forests from an animal perspective. However, for managers, it is also important to identify how many ungulates a forest can handle before forest regeneration is compromised. Our results suggest a crucial role of ungulate density in forest regeneration, structure, and functioning. At low ungulate density forest regeneration, structure and functioning are maintained, whereas at intermediate to high ungulate densities the different forest attributes are negatively affected.

## Acknowledgements

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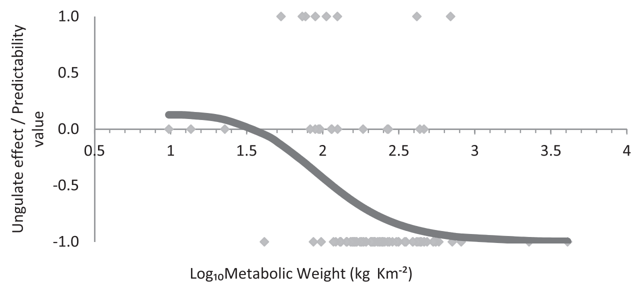
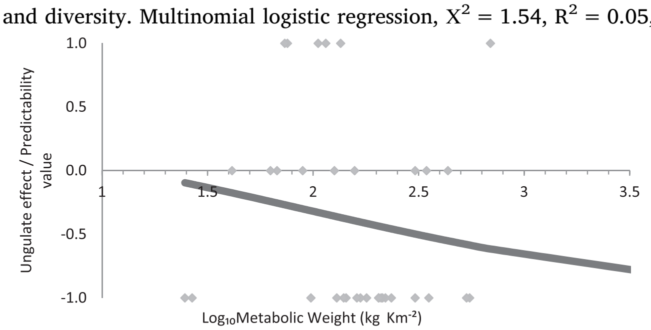
**A**

### *A.1 Multinomial regression curves for forest regeneration*

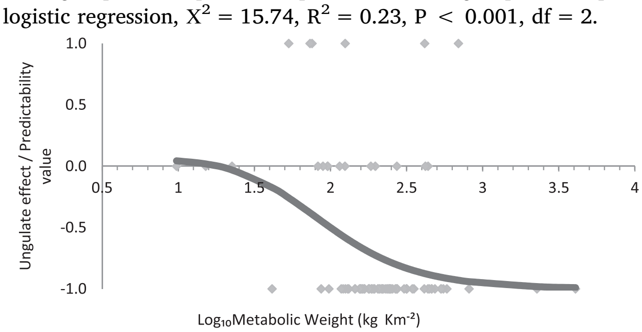
Abundance refers to the amount of seedling, saplings and poles in the forest. Multinomial logistic regression, $X^2 = 21.33$, $R^2 = 0.25$, $P < 0.001$, df = 2.




Diversity refers to species richness and diversity. Multinomial logistic regression, $X^2 = 1.54$, $R^2 = 0.05$, $P < 0.463$, df = 2.

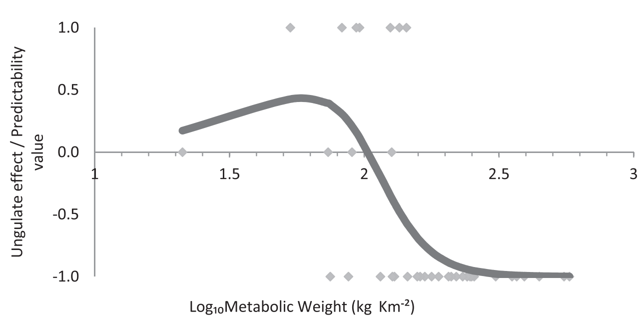



Composition refers to the proportion of a group of tree species compared to another group of tree species. Literature often compares conifer and broadleaved proportions. Multinomial logistic regression, $X^2 = 15.74$, $R^2 = 0.23$, $P < 0.001$, df = 2.

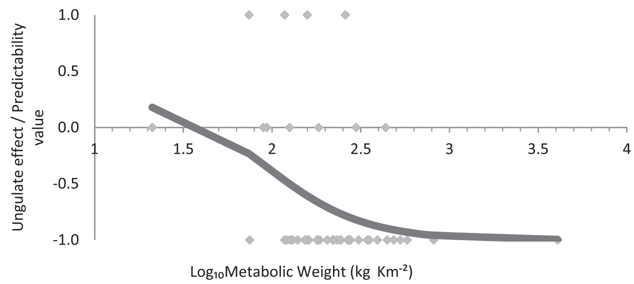



### *A.2. Multinomial regression curves for forest structure*

Horizontal structure refers to the range and distribution of tree species in a forest. Multinomial logistic regression, $X^2 = 22.66$, $R^2 = 0.57$ $P < 0.001$, df = 2.

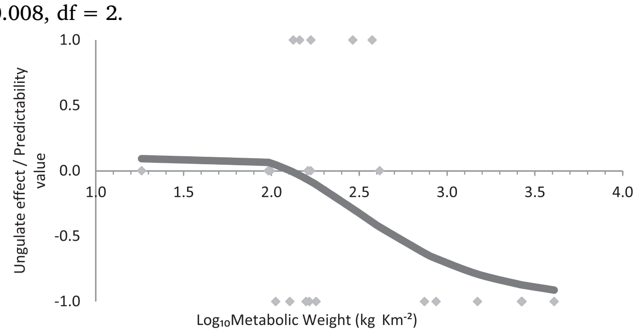



Vertical structure refers to the vertical layering of the forest, which includes undergrowth, understorey, canopy and emergent layer. Multinomial logistic regression, $X^2 = 7.28$, $R^2 = 0.20$ $P = 0.026$, df = 2.

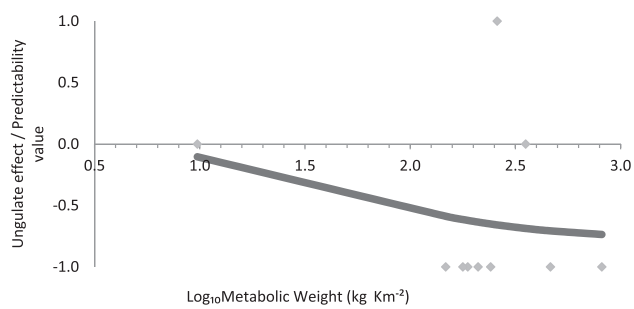



*A.3. Multinomial regression curves for forest functioning*

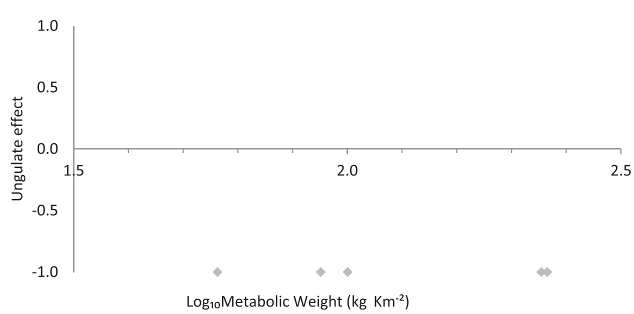
Nutrient cycling in soil refers to disruption of the processes related to the formation of soil and nutrient availability. Multinomial logistic regression, $X^2 = 9.57$, $R^2 = 0.39$ $P = 0.008$, df = 2.




Tree growth refers mainly to the amount of woody biomass produced by trees. Multinomial logistic regression, $X^2 = 2.55$, $R^2 = 0.28$ $P = 0.279$, df = 2.




Wild food refers to the provision of wild food on forests, example fruits and nuts. Predicted regression curve does not apply due to insufficient sample size.




## B

*B.1. List of papers reviewed*

Abrams, M. D. (2003). Where has all the white oak gone? Bioscience, 53(10), 927–939. doi: https://doi.org//10.1641/0006-3568(2003)053[0927:whatwo]2.0.co;2

Abrams, M. D., Copenheaver, C. A., Terazawa, K., Umeki, K., Takiya, M., & Akashi, N. (1999). A 370-year dendroecological history of an old-growth Abies-Acer-Quercus forest in Hokkaido, northern Japan. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 29(12), 1891–1899. doi: https://doi.org//10.1139/cjfr-29-12-1891

Abrams, M. D., & Orwig, D. A. (1996). A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. Journal of Ecology, 84(3), 353–363. doi: https://doi.org//10.2307/2261198

Abrams, M. D., van de Gavel, S., Dodson, R. C., & Copenheaver, C. A. (2000). The dendroecology and climatic impacts for old-growth white pine and hemlock on the extreme slopes of the Berkshire Hills, Massachusetts, USA. Canadian Journal of Botany-Revue Canadienne De Botanique, 78(7), 851–861.
Akashi, N., & Nakashizuka, T. (1999). Effects of bark-stripping by Sika deer (Cervus nippon) on population dynamics of a mixed forest in Japan. Forest Ecology and Management, 113(1), 75–82. doi: https://doi.org//10.1016/s0378-1127(98)00415-0
Akashi, N., Unno, A., & Terazawa, K. (2015). Significance of woody browse preferences in evaluating the impact of sika deer browsing on tree seedlings. Journal of Forest Research, 20(4), 396–402. doi: https://doi.org//10.1007/s10310-015-0492-3
Allombert, S., Gaston, A. J., & Martin, J. L. (2005). A natural experiment on the impact of overabundant deer on songbird populations. Biological Conservation, 126(1), 1–13. doi: https://doi.org//10.1016/j.biocon.2005.04.001
Allombert, S., Stockton, S., & Martin, J. L. (2005). A natural experiment on the impact of overabundant deer on forest invertebrates. Conservation Biology, 19(6), 1917–1929. doi: https://doi.org//10.1111/j.1523-1739.2005.00280.x
Ammer, C. (1996). Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. Forest Ecology and Management, 88(1–2), 43–53. doi: https://doi.org//10.1016/s0378-1127(96)03808-x
Anderson, R. C., Corbett, E. A., Anderson, M. R., Corbett, G. A., & Kelley, T. M. (2001). High white-tailed deer density has negative impact on tallgrass prairie forbs. Journal of the Torrey Botanical Society, 128(4), 381–392. doi: https://doi.org//10.2307/3088670
Asnani, K. M., Klips, R. A., & Curtis, P. S. (2006). Regeneration of woodland vegetation after deer browsing in Sharon Woods Metro Park, Franklin County, Ohio. Ohio Journal of Science, 106(3), 86–92.
Augustine, D. J., & Frelich, L. E. (1998). Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology, 12(5), 995–1004. doi: https://doi.org//10.1046/j.1523-1739.1998.97248.x
Barancekova, M., Krojerova-Prokesova, J., & Homolka, M. (2007). Impact of deer browsing on natural and artificial regeneration in floodplain forest. Folia Zoologica, 56(4), 354–364.
Barrios-Garcia, M. N., Relva, M. A., & Kitzberger, T. (2012). Patterns of use and damage by exotic deer on native plant communities in northwestern Patagonia. European Journal of Wildlife Research, 58(1), 137–146. doi: https://doi.org//10.1007/s10344-011-0554-6
Bassett, I., Simcock, R., & Mitchell, N. (2005). Consequences of soil compaction for seedling establishment: Implications for natural regeneration and restoration. Austral Ecology, 30(8), 827–833.
Beauchamp, V. B., Ghuznavi, N., Koontz, S. M., & Roberts, R. P. (2013). Edges, exotics and deer: the seed bank of a suburban secondary successional temperate deciduous forest. Applied Vegetation Science, 16(4), 571–584. doi: https://doi.org//10.1111/avsc.12036
Bellingham, P. J., & Allan, C. N. (2003). Forest regeneration and the influences of white-tailed deer (Odocoileus virginianus) in cool temperate New Zealand rain forests. Forest Ecology and Management, 175(1–3), 71–86. doi: https://doi.org//10.1016/s0378-1127(02)00122-6
Beschta, R. L., & Ripple, W. J. (2008). Wolves, trophic cascades, and rivers in the Olympic National Park, USA. Ecohydrology, 1(2), 118–130. doi: https://doi.org//10.1002/eco.12
Blackhall, M., Veblen, T. T., & Raffaele, E. (2015). Recent fire and cattle herbivory enhance plant-level fuel flammability in shrublands. Journal of Vegetation Science, 26(1), 123–133. doi: https://doi.org//10.1111/jvs.12216
Bork, E. W., Carlyle, C. N., Cahill, J. F., Haddow, R. E., & Hudson, R. J. (2013). Disentangling herbivore impacts on Populus tremuloides: a comparison of native ungulates and cattle in Canada's Aspen Parkland. Oecologia, 173(3), 895–904. doi: https://doi.org//10.1007/s00442-013-2676-x
Bork, E. W., Hudson, R. J., & Bailey, A. W. (1997). Populus forest characterization in Elk Island National Park relative to herbivory, prescribed fire, and topography. Canadian Journal of Botany-Revue Canadienne De Botanique, 75(9), 1518–1526.
Boucher, S., Crete, M., Ouellet, J. P., Daigle, C., & Lesage, L. (2004). Large-scale trophic interactions: White-tailed deer growth and forest understory. Ecoscience, 11(3), 286–295.
Boulanger, V., Baltzinger, C., Said, S., Ballon, P., Ningre, F., Picard, J. F., & Dupouey, J. L. (2011). Deer-mediated expansion of a rare plant species. Plant Ecology, 212(2), 307–314. doi: https://doi.org//10.1007/s11258-010-9823-9
Bowman, D., & Panton, W. J. (1991). SIGN AND HABITAT IMPACT OF BANTENG (BOS-JAVANICUS) AND PIG (SUS-SCROFA), COBOURG PENINSULA, NORTHERN AUSTRALIA. Australian Journal of Ecology, 16(1), 15–17. doi: https://doi.org//10.1111/j.1442-9993.1991.tb01477.x
Bruinderink, G. G., & Hazebroek, E. (1996). Wild boar (Sus scrofa scrofa L.) rooting and forest regeneration on podzolic soils in the Netherlands. Forest Ecology and Management, 88(1), 71–80.
Brullhardt, M., Risch, A. C., Filli, F., Haller, R. M., & Schutz, M. (2015). Spatiotemporal dynamics of natural tree regeneration in unmanaged subalpine conifer forests with high wild ungulate densities. Canadian Journal of Forest Research, 45(6), 607–614. doi: https://doi.org//10.1139/cjfr-2014-0358
Buesching, C. D., Newman, C., Jones, J. T., & Macdonald, D. W. (2011). Testing the effects of deer grazing on two woodland rodents, bankvoles and woodmice. Basic and Applied Ecology, 12(3), 207–214. doi: https://doi.org//10.1016/j.baae.2011.02.007
Callan, R., Nibbelink, N. P., Rooney, T. P., Wiedenhoeft, J. E., & Wydeven, A. P. (2013). Recolonizing wolves trigger a trophic cascade in Wisconsin (USA). Journal of Ecology, 101(4), 837–845. doi: https://doi.org//10.1111/1365-2745.12095
Cardinal, E., Martin, J. L., & Cote, S. D. (2012). Large herbivore effects on songbirds in boreal forests: lessons from deer introduction on Anticosti Island. Ecoscience, 19(1), 38–47. doi: https://doi.org//10.2980/19-1-3441
Carson, W. P., Banta, J. A., Royo, A. A., & Kirschbaum, C. (2005). Plant communities growing on boulders in the Allegheny National Forest: Evidence for boulders as refugia from deer and as a bioassay of overbrowsing. Natural Areas Journal, 25(1), 10–18.
Chen, J. R., Wang, Q. L., Li, M., Liu, F., Li, W., & Yin, L. Y. (2013). Effects of deer disturbance on soil respiration in a subtropical floodplain wetland of the Yangtze River. European Journal of Soil Biology, 56, 65–71. doi: https://doi.org//10.1016/j.ejsobi.2013.02.007
Chollet, S., Baltzinger, C., Ostermann, L., Saint-Andre, F., & Martin, J. L. (2013). Importance for forest plant communities of refuges protecting from deer browsing. Forest Ecology and Management, 289, 470–477. doi: https://doi.org//10.1016/j.foreco.2012.10.043
Chollet, S., Bergman, C., Gaston, A. J., & Martin, J. L. (2015). Long-term consequences of invasive deer on songbird communities: Going from bad to worse? Biological Invasions, 17(2), 777–790. doi: https://doi.org//10.1007/s10530-014-0768-0
Comisky, L., Royo, A. A., & Carson, W. P. (2005). Deer browsing creates rock refugia gardens on large boulders in the Allegheny National Forest, Pennsylvania. American Midland Naturalist, 154(1), 201–206. doi: https://doi.org//10.1674/0003-0031(2005)154[0201:dbcrrg]2.0.co;2
De Jong, C., Gill, R., Van Wieren, S., & Burlton, F. (1995). Diet selection by roe deer Capreolus capreolus in Kielder Forest in relation to plant

cover. Forest Ecology and Management, 79(1), 91–97.
Diaci, J., Rozenbergar, D., Anic, I., Mikac, S., Saniga, M., Kucbel, S., … Ballian, D. (2011). Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. Forestry, 84(5), 479–491. doi: https://doi.org//10.1093/forestry/cpr030
Didier, K. A., & Porter, W. F. (2003). Relating spatial patterns of sugar maple reproductive success and relative deer density in northern New York State. Forest Ecology and Management, 181(1–2), 253–266. doi: https://doi.org//10.1016/s0378-1127(03)00137-3
Diwold, K., Dullinger, S., & Dirnbock, T. (2010). Effect of nitrogen availability on forest understorey cover and its consequences for tree regeneration in the Austrian limestone Alps. Plant Ecology, 209(1), 11–22. doi: https://doi.org//10.1007/s11258-009-9715-z
Eschtruth, A. K., & Battles, J. J. (2008). Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. Ecological Applications, 18(2), 360–376. doi: https://doi.org//10.1890/07-0446.1
Eycott, A. E., Watkinson, A. R., Hemami, M. R., & Dolman, P. M. (2007). The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. Oecologia, 154(1), 107–118. doi: https://doi.org//10.1007/s00442-007-0812-1
Filazzola, A., Tanentzap, A. J., & Bazely, D. R. (2014). Estimating the impacts of browsers on forest understories using a modified index of community composition. Forest Ecology and Management, 313, 10–16. doi: https://doi.org//10.1016/j.foreco.2013.10.040
Fisichelli, N., Frelich, L. E., & Reich, P. B. (2012). Sapling growth responses to warmer temperatures 'cooled' by browse pressure. Global Change Biology, 18(11), 3455–3463. doi: https://doi.org//10.1111/j.1365-2486.2012.02785.x
Fisichelli, N. A., Frelich, L. E., Reich, P. B., & Eisenhauer, N. (2013). Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. Biological Invasions, 15(5), 1057–1066. doi: https://doi.org//10.1007/s10530-012-0350-6
Forsyth, D. M., Wilson, D. J., Easdale, T. A., Kunstler, G., Canham, C. D., Ruscoe, W. A., … Coomes, D. A. (2015). Century-scale effects of invasive deer and rodents on the dynamics of forests growing on soils of contrasting fertility. Ecological Monographs, 85(2), 157–180. doi: https://doi.org//10.1890/14-0389.1.sm
Frerker, K., Sabo, A., & Waller, D. (2014). Long-Term Regional Shifts in Plant Community Composition Are Largely Explained by Local Deer Impact Experiments. Plos One, 9(12), 17. doi: https://doi.org//10.1371/journal.pone.0115843
Frerker, K., Sonnier, G., & Waller, D. M. (2013). Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. Forest Ecology and Management, 291, 55–64. doi: https://doi.org//10.1016/j.foreco.2012.11.041
Furedi, M., & McGraw, J. B. (2004). White-tailed deer: Dispersers or predators of American ginseng seeds? American Midland Naturalist, 152(2), 268–276. doi: https://doi.org//10.1674/0003-0031(2004)152[0268:wddopo]2.0.co;2
Genov, P. V., & Massei, G. (2004). The environmental impact of wild boar. Galemys: Boletín informativo de la Sociedad Española para la conservación y estudio de los mamíferos, 16(1), 135–145.
Gill, R., & Beardall, V. (2001). The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry, 74(3), 209–218.
Gill, R., & Morgan, G. (2010). The effects of varying deer density on natural regeneration in woodlands in lowland Britain. Forestry, 83(1), 53–63.
Goetsch, C., Wigg, J., Royo, A. A., Ristau, T., & Carson, W. P. (2011). Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: Results from a 60 year-old deer exclusion plot. Journal of the Torrey Botanical Society, 138(2), 220–224.
Gomez, J. M., Garcia, D., & Zamora, R. (2003). Impact of vertebrate acorn- and seedling-predators on a Mediterranean Quercus pyrenaica forest. Forest Ecology and Management, 180(1–3), 125–134. doi: https://doi.org//10.1016/s0378-1127(02)00608-4
Gotmark, F. G., Berglund, A., & Wiklander, K. (2005). Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. Scandinavian Journal of Forest Research, 20(3), 223–234. doi: https://doi.org//10.1080/02827580510008383
Haaverstad, O., Hjeljord, O., & Wam, H. K. (2014). Wild boar rooting in a northern coniferous forest - minor silviculture impact. Scandinavian Journal of Forest Research, 29(1), 90–95. doi: https://doi.org//10.1080/02827581.2013.865781
Hanberry, P., Hanberry, B. B., Demarais, S., Leopold, B. D., & Fleeman, J. (2014). Impact on plant communities by white-tailed deer in Mississippi, USA. Plant Ecology & Diversity, 7(4), 541–548. doi: https://doi.org//10.1080/17550874.2013.842615
Harmer, R. (2001). The effect of plant competition and simulated summer browsing by deer on tree regeneration. Journal of Applied Ecology, 38(5), 1094–1103. doi: https://doi.org//10.1046/j.1365-2664.2001.00664.x
Heckel, C. D., Bourg, N. A., McShea, W. J., & Kalisz, S. (2010). Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. Ecology, 91(2), 319–326.
Hedl, R., Kopecky, M., & Komarek, J. (2010). Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Diversity and Distributions, 16(2), 267–276. doi: https://doi.org//10.1111/j.1472-4642.2010.00637.x
Henden, J. A., Ims, R. A., Yoccoz, N. G., & Killengreen, S. T. (2011). Declining willow ptarmigan populations: The role of habitat structure and community dynamics. Basic and Applied Ecology, 12(5), 413–422. doi: https://doi.org//10.1016/j.baae.2011.05.006
Heuze, P., Schnitzler, A., & Klein, F. (2005). Consequences of increased deer browsing winter on silver fir and spruce regeneration in the Southern Vosges mountains: Implications for forest management. Annals of Forest Science, 62(2), 175–181. doi: https://doi.org//10.1051/forest:2005009
Holm, J. A., Thompson, J. R., McShea, W. J., & Bourg, N. A. (2013). Interactive effects of chronic deer browsing and canopy gap disturbance on forest successional dynamics. Ecosphere, 4(11), 23. doi: https://doi.org//10.1890/es13-00223
Holmes, S. A., Curran, L. M., & Hall, K. R. (2008). White-tailed deer (Odocoileus virginianus) alter herbaceous species richness in the Hiawatha National Forest, Michigan, USA. American Midland Naturalist, 159(1), 83–97. doi: https://doi.org//10.1674/0003-0031(2008)159[83:wdovah]2.0.co;2
Holmes, S. A., Webster, C. R., Flaspohler, D. J., & Froese, R. E. (2009). Death and Taxus: the high cost of palatability for a declining evergreen shrub, Taxus canadensis. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 39(7), 1366–1374. doi: https://doi.org//10.1139/x09-064
Holt, C. A., Fuller, R. J., & Dolman, P. M. (2011). Breeding and post-breeding responses of woodland birds to modification of habitat structure by deer. Biological Conservation, 144(9), 2151–2162. doi: https://doi.org//10.1016/j.biocon.2011.05.004
Hornberg, S. (2001). Changes in population density of moose (Alces alces) and damage to forests in Sweden. Forest Ecology and Management, 149(1–3), 141–151. doi: https://doi.org//10.1016/s0378-1127(00)00551-x
Horsley, S. B., Stout, S. L., & DeCalesta, D. S. (2003). White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications, 13(1), 98–118. doi: https://doi.org//10.1890/1051-0761(2003)013[0098:wtdiot]2.0.co;2

Husheer, S. W., Allen, R. B., & Robertson, A. W. (2006). Suppression of regeneration in New Zealand mountain beech forests is dependent on species of introduced deer. Biological Invasions, 8(4), 823–834. doi: https://doi.org//10.1007/s10530-005-4011-x
Husheer, S. W., Coomes, D. A., & Robertson, A. W. (2003). Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. Forest Ecology and Management, 181(1–2), 99–117. doi: https://doi.org//10.1016/s0378-1127(03)00120-8
Husheer, S. W., & Frampton, C. M. (2005). Fallow deer impacts on Wakatipu beech forest. New Zealand Journal of Ecology, 29(1), 83–94.
Husheer, S. W., Hansen, Q. W., & Urlich, S. C. (2005). Effects of red deer on tree regeneration and growth in Aorangi Forest, Wairarapa. New Zealand Journal of Ecology, 29(2), 271–277.
Ito, H., & Hino, T. (2008). Effects of deer and mice on seedling survival in a temperate mixed forest of Japan. Forest Ecology and Management, 256(1–2), 129–135. doi: https://doi.org//10.1016/j.foreco.2008.04.016
Joys, A. C., Fuller, R. J., & Dolman, P. M. (2004). Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England. Forest Ecology and Management, 202(1–3), 23–37. doi: https://doi.org//10.1016/j.foreco.2004.06.035
Kain, M., Battaglia, L., Royo, A., & Carson, W. P. (2011). Over-browsing in Pennsylvania creates a depauperate forest dominated by an understory tree: Results from a 60-year-old deer exclosure. Journal of the Torrey Botanical Society, 138(3), 322–326.
Kalisz, S., Spigler, R. B., & Horvitz, C. C. (2014). In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. Proceedings of the National Academy of Sciences of the United States of America, 111(12), 4501–4506. doi: https://doi.org//10.1073/pnas.1310121111
Kamler, J., Homolka, M., Barancekova, M., & Krojerova-Prokesova, J. (2010). Reduction of herbivore density as a tool for reduction of herbivore browsing on palatable tree species. European Journal of Forest Research, 129(2), 155–162. doi: https://doi.org//10.1007/s10342-009-0309-z
Kay, S. (1993). Factors affecting severity of deer browsing damage within coppiced woodlands in the south of England. Biological Conservation, 63(3), 217–222.
Kern, C. C., Reich, P. B., Montgomery, R. A., & Strong, T. F. (2012). Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? Forest Ecology and Management, 267, 134–143. doi: https://doi.org//10.1016/j.foreco.2011.12.002
Kirschbaum, C. D., & Anacker, B. L. (2005). The utility of Trillium and Maianthemum as phyto-indicators of deer impact in northwestern Pennsylvania, USA. Forest Ecology and Management, 217(1), 54–66. doi: https://doi.org//10.1016/j.foreco.2005.05.001
Kisanuki, H., Nakasu, M., Nakai, A., & Yurugi, Y. (2008). Predicting the population dynamics of three understory broad-leaved evergreen species under the influence of Sika deer in primary and secondary forests of mid-western Japan. Journal of Forest Research, 13(1), 52–58. doi: https://doi.org//10.1007/s10310-007-0054-4
Klopcic, M., Jerina, K., & Boncina, A. (2010). Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? European Journal of Forest Research, 129(3), 277–288. doi: https://doi.org//10.1007/s10342-009-0325-z
Knight, T. M., Dunn, J. L., Smith, L. A., Davis, J., & Kalisz, S. (2009). Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal, 29(2), 110–116.
Koda, R., & Fujita, N. (2011). Is deer herbivory directly proportional to deer population density? Comparison of deer feeding frequencies among six forests with different deer density. Forest Ecology and Management, 262(3), 432–439. doi: https://doi.org//10.1016/j.foreco.2011.04.009
Kraft, L. S., Crow, T. R., Buckley, D. S., Nauertz, E. A., & Zasada, J. C. (2004). Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. Forest Ecology and Management, 199(2–3), 219–230. doi: https://doi.org//10.1016/j.foreco.2004.05.044
Kuijper, D. P. J., Cromsigt, J., Jedrzejewska, B., Miscicki, S., Churski, M., Jedrzejewski, W., & Kweczlich, I. (2010). Bottom-up versus top-down control of tree regeneration in the Bialowieza Primeval Forest, Poland. Journal of Ecology, 98(4), 888–899. doi: https://doi.org//10.1111/j.1365-2745.2010.01656.x
Kuijper, D. P. J., Jedrzejewska, B., Brzeziecki, B., Churski, M., Jedrzejewski, W., & Zybura, H. (2010). Fluctuating ungulate density shapes tree recruitment in natural stands of the Bialowieza Primeval Forest, Poland. Journal of Vegetation Science, 21(6), 1082–1098. doi: https://doi.org//10.1111/j.1654-1103.2010.01217.x
Kuiters, A. T., & Slim, P. A. (2002). Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation, 105(1), 65–74. doi: https://doi.org//10.1016/s0006-3207(01)00204-x
Kullberg, Y., & Bergstrom, R. (2001). Winter browsing by large herbivores on planted deciduous seedlings in southern Sweden. Scandinavian Journal of Forest Research, 16(4), 371–378. doi: https://doi.org//10.1080/02827580152496768
Kumar, S., Takeda, A., & Shibata, E. (2006). Effects of 13-year fencing on browsing by sika deer on seedlings on Mt. Ohdaigahara, central Japan. Journal of Forest Research, 11(5), 337–342. doi: https://doi.org//10.1007/s10310-006-0216-9
Kumbasli, M., Makineci, E., & Cakir, M. (2010). Long term effects of red deer (Cervus elaphus) grazing on soil in a breeding area. Journal of Environmental Biology, 31(1–2), 185–188.
Laskurain, N. A., Aldezabal, A., Olano, J. M., Loidi, J., & Escudero, A. (2013). Intensification of domestic ungulate grazing delays secondary forest succession: evidence from exclosure plots. Journal of Vegetation Science, 24(2), 320–331. doi: https://doi.org//10.1111/j.1654-1103.2012.01469.x
Liang, S. Y., & Seagle, S. W. (2002). Browsing and microhabitat effects on riparian forest woody seedling demography. Ecology, 83(1), 212–227. doi: https://doi.org//10.2307/2680133
Ligot, G., Gheysen, T., Lehaire, F., Hebert, J., Licoppe, A., Lejeune, P., & Brostaux, Y. (2013). Modeling recent bark stripping by red deer (Cervus elaphus) in South Belgium coniferous stands. Annals of Forest Science, 70(3), 309–318. doi: https://doi.org//10.1007/s13595-012-0253-9
Long, R. P., Brose, P. H., & Horsley, S. B. (2012). Responses of northern red oak seedlings to lime and deer exclosure fencing in Pennsylvania. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 42(4), 698–709. doi: https://doi.org//10.1139/x2012-025
Long, Z. T., Pendergast, T. H., & Carson, W. P. (2007). The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. Forest Ecology and Management, 252(1–3), 230–238. doi: https://doi.org//10.1016/j.foreco.2007-06.034
Lucas, R. W., Salguero-Gomez, R., Cobb, D. B., Waring, B. G., Anderson, F., McShea, W. J., & Casper, B. B. (2013). White-tailed deer (Odocoileus virginianus) positively affect the growth of mature northern red oak (Quercus rubra) trees. Ecosphere, 4(7), 15. doi: https://doi.org//10.1890/es13-00036.1

Lyly, M., Klemola, T., Koivisto, E., Huitu, O., Oksanen, L., & Korpimaki, E. (2014). Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings. Oecologia, 174(1), 271–281. doi: https://doi.org//10.1007/s00442-013-2761-1
Mansson, J., & Jarnemo, A. (2013). Bark-stripping on Norway spruce by red deer in Sweden: level of damage and relation to tree characteristics. Scandinavian Journal of Forest Research, 28(2), 117–125. doi: https://doi.org//10.1080/02827581.2012.701323
Mansson, J., Kalen, C., Kjellander, P., Andren, H., & Smith, H. (2007). Quantitative estimates of tree species selectivity by moose (Alces alces) in a forest landscape. Scandinavian Journal of Forest Research, 22(5), 407–414. doi: https://doi.org//10.1080/02827580701515023
Martin, J. L., & Baltzinger, C. (2002). Interaction among deer browsing, hunting, and tree regeneration. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 32(7), 1254–1264. doi: https://doi.org//10.1139/x02-043
Martin, T. G., Arcese, P., & Scheerder, N. (2011). Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. Biological Conservation, 144(1), 459–469. doi: https://doi.org//10.1016/j.biocon.2010.09.033
Mathisen, K. M., Buhtz, F., Danell, K., Bergstrom, R., Skarpe, C., Suominen, O., & Persson, I. L. (2010). Moose density and habitat productivity affects reproduction, growth and species composition in field layer vegetation. Journal of Vegetation Science, 21(4), 705–716. doi: https://doi.org//10.1111/j.1654-1103.2010.01180.x
Matonis, M. S., Walters, M. B., & Millington, J. D. A. (2011). Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. Forest Ecology and Management, 262(2), 286–298. doi: https://doi.org//10.1016/j.foreco.2011.03.034
McColley, S. D., Tyers, D. B., & Sowell, B. F. (2012). Aspen and Willow Restoration Using Beaver on the Northern Yellowstone Winter Range. Restoration Ecology, 20(4), 450–455. doi: https://doi.org//10.1111/j.1526-100X.2011.00792.x
McGarvey, J. C., Bourg, N. A., Thompson, J. R., McShea, W. J., & Shen, X. L. (2013). Effects of Twenty Years of Deer Exclusion on Woody Vegetation at Three Life-History Stages in a Mid-Atlantic Temperate Deciduous Forest. Northeastern Naturalist, 20(3), 451–468. doi: https://doi.org//10.1656/045.020.0301
McGraw, J. B., & Furedi, M. A. (2005). Deer browsing and population viability of a forest understory plant. Science, 307(5711), 920–922. doi: https://doi.org//10.1126/science.1107036
McShea, W. J., & Rappole, J. H. (2000). Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology, 14(4), 1161–1170. doi: https://doi.org//10.1046/j.1523-1739.2000.99210.x
Merli, E., & Meriggi, A. (2006). Using harvest data to predict habitat-population relationship of the wild boar Sus scrofa in Northern Italy. Acta Theriologica, 51(4), 383–394. doi: https://doi.org//10.1007/bf03195185
Metslaid, M., Koster, K., Jogiste, K., Randveer, T., Voolma, K., & Moser, W. K. (2013). The Effect of Simulated Bark Stripping by Moose on Scots Pine Height Growth: an Experimental Treatment. Baltic Forestry, 19(1), 61–66.
Michels, G. H., Vieira, E. M., & de Sa, F. N. (2012). Short- and long-term impacts of an introduced large herbivore (Buffalo, Bubalus bubalis L.) on a neotropical seasonal forest. European Journal of Forest Research, 131(4), 965–976. doi: https://doi.org//10.1007/s10342-011-0568-3
Millington, J. D. A., Walters, M. B., Matonis, M. S., Laurent, E. J., Hall, K. R., & Liu, J. G. (2011). Combined long-term effects of variable tree regeneration and timber management on forest songbirds and timber production. Forest Ecology and Management, 262(5), 718–729. doi: https://doi.org//10.1016/j.foreco.2011.05.002
Millington, J. D. A., Walters, M. B., Matonis, M. S., & Liu, J. G. (2013). Modelling for forest management synergies and trade-offs: Northern hardwood tree regeneration, timber and deer. Ecological Modelling, 248, 103–112. doi: https://doi.org//10.1016/j.ecolmodel.2012.09.019
Monzon, A., da Silva, S. V., & Manso, F. T. (2012). Integrating the deer (Cervus elaphus) in the Portuguese forests: Impacts and new challenges for forest certification. Forest Ecology and Management, 267, 1–6. doi: https://doi.org//10.1016/j.foreco.2011.11.042
Moser, B., Schutz, M., & Hindenlang, K. E. (2006). Importance of alternative food resources for browsing by roe deer on deciduous trees: The role of food availability and species quality. Forest Ecology and Management, 226(1–3), 248–255. doi: https://doi.org//10.1016/j.foreco.2006.01.045
Motta, R. (2003). Ungulate impact on rowan (Sorbus aucuparia L.) and Norway spruce (Picea abies (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. Forest Ecology and Management, 181(1–2), 139–150. doi: https://doi.org//10.1016/s0378-1127(03)00128-2
Murata, I., Saruki, S., Kubota, K., Inoue, S., Tashiro, N., Enoki, T., … Inoue, S. (2009). Effects of sika deer (Cervus nippon) and dwarf bamboo (Sasamorpha borealis) on seedling emergence and survival in cool-temperate mixed forests in the Kyushu Mountains. Journal of Forest Research, 14(5), 296–301. doi: https://doi.org//10.1007/s10310-009-0131-y
Murphy, M. J., Inman-Narahari, F., Ostertag, R., & Litton, C. M. (2014). Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. Biological Invasions, 16(1), 63–71. doi: https://doi.org//10.1007/s10530-013-0503-2
Murray, B. D., Webster, C. R., & Bump, J. K. (2013). Broadening the ecological context of ungulate-ecosystem interactions: the importance of space, seasonality, and nitrogen. Ecology, 94(6), 1317–1326.
Murray, B. D., Webster, C. R., & Bump, J. K. (2014). A Migratory Ungulate Facilitates Cross-Boundary Nitrogen Transport in Forested Landscapes. Ecosystems, 17(6), 1002–1013. doi: https://doi.org//10.1007/s10021-014-9796-y
Mysterud, A., & Østbye, E. (2004). Roe deer (Capreolus capreolus) browsing pressure affects yew (Taxus baccata) recruitment within nature reserves in Norway. Biological Conservation, 120(4), 545–548.
Naaf, T., & Wulf, M. (2007). Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. Forest Ecology and Management, 244(1–3), 141–149. doi: https://doi.org//10.1016/j.foreco.2007.04.020
Niwa, S., Mariani, L., Kaneko, N., Okada, H., & Sakamoto, K. (2011). Early-stage impacts of sika deer on structure and function of the soil microbial food webs in a temperate forest: A large-scale experiment. Forest Ecology and Management, 261(3), 391–399. doi: https://doi.org//10.1016/j.foreco.2010.10.024
Nomiya, H., Suzuki, W., Kanazashi, T., Shibata, M., Tanaka, H., & Nakashizuka, T. (2003). The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. Plant Ecology, 164(2), 263–276. doi: https://doi.org//10.1023/a:1021294021438
Nunez, M. A., Relva, M. A., & Simberloff, D. (2008). Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria, Argentina. Austral Ecology, 33(3), 317–323. doi: https://doi.org//10.1111/j.1442-9993.2007.01819.x
Nuttle, T., Ristau, T. E., & Royo, A. A. (2014). Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology, 102(1), 221–228. doi: https://doi.org//10.1111/1365-2745.12175

Olesen, C. R., & Madsen, P. (2008). The impact of roe deer (Capreolus capreolus), seedbed, light and seed fall on natural beech (Fagus sylvatica) regeneration. Forest Ecology and Management, 255(12), 3962–3972. doi: https://doi.org//10.1016/j.foreco.2008.03.050

Patel, A., & Rapport, D. J. (2000). Assessing the impacts of deer browsing, prescribed burns, visitor use, and trails on an oak-pine forest: Pinery Provincial Park, Ontario, Canada. Natural Areas Journal, 20(3), 250–260.

Pellerin, M., Said, S., Richard, E., Hamann, J. L., Dubois-Coli, C., & Hum, P. (2010). Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. Forest Ecology and Management, 260(4), 429–437. doi: https://doi.org//10.1016/j.foreco.2010.04.031

Pepin, D., Renaud, P. C., Boscardin, Y., Goulard, A., Mallet, C., Anglard, F., & Ballon, P. (2006). Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings - An enclosure-based experiment. Forest Ecology and Management, 222(1–3), 302–313. doi: https://doi.org//10.1016/j.foreco.2005.10.034

Perea, R., Girardello, M., & San Miguel, A. (2014). Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. Biodiversity and Conservation, 23(5), 1303–1318. doi: https://doi.org//10.1007/s10531-014-0666-x

Persson, I. L., Pastor, J., Danell, K., & Bergstrom, R. (2005). Impact of moose population density on the production and composition of litter in boreal forests. Oikos, 108(2), 297–306. doi: https://doi.org//10.1111/j.0030-1299.2005.13844.x

Powers, M. D., & Nagel, L. M. (2009). Pennsylvania sedge cover, forest management and Deer density influence tree regeneration dynamics in a northern hardwood forest. Forestry, 82(3), 241–254. doi: https://doi.org//10.1093/forestry/cpp003

Prietzel, V. J., & Ammer, C. (2008). Mixed mountain forests of the Bavarian Limestone Alps: Reduction of ungulate density results not only in increased regeneration success but also in improved soil fertility. Allgemeine Forst Und Jagdzeitung, 179(5–6), 104–112.

Reimoser, F., & Gossow, H. (1996). Impact of ungulates on forest vegetation and its dependence on the silvicultural system. Forest Ecology and Management, 88(1–2), 107–119. doi: https://doi.org//10.1016/s0378-1127(96)03816-9

Relva, M. A., Castan, E., & Mazzarino, M. J. (2014). Litter and soil properties are not altered by invasive deer browsing in forests of NW Patagonia. Acta Oecologica-International Journal of Ecology, 54, 45–50. doi: https://doi.org//10.1016/j.actao.2012.12.006

Relva, M. A., Nunez, M. A., & Simberloff, D. (2010). Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biological Invasions, 12(2), 303–311. doi: https://doi.org//10.1007/s10530-009-9623-0

Relva, M. A., & Veblen, T. T. (1998). Impacts of introduced large herbivores on Austrocedrus chilensis forests in northern Patagonia, Argentina. Forest Ecology and Management, 108(1–2), 27–40. doi: https://doi.org//10.1016/s0378-1127(97)00313-7

Richer, M. C., Ouellet, J. P., Lapointe, L., Crete, A., & Huot, J. (2005). Impacts of white-tailed deer grazing in hay fields of southern Quebec. Wildlife Society Bulletin, 33(4), 1274–1281. doi: https://doi.org//10.2193/0091-7648(2005)33[1274:iowdgi]2.0.co;2

Rogers, P. C., & Mittanck, C. M. (2014). Herbivory strains resilience in drought-prone aspen landscapes of the western United States. Journal of Vegetation Science, 25(2), 457–469. doi: https://doi.org//10.1111/jvs.12099

Rogerson, J. E., Bowman, J. L., Tymkiw, E. L., Colligan, G. M., & Vasilas, B. L. (2014). The Impacts of White-Tailed Deer Browsing and Distance From the Forest Edge on Soybean Yield. Wildlife Society Bulletin, 38(3), 473–479. doi: https://doi.org//10.1002/wsb.442

Rooney, T. P., & Gross, K. (2003). A demographic study of deer browsing impacts on Trillium grandiflorum. Plant Ecology, 168(2), 267–277. doi: https://doi.org//10.1023/a:1024486606698

Royo, A. A., Collins, R., Adams, M. B., Kirschbaum, C., & Carson, W. P. (2010). Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology, 91(1), 93–105. doi: https://doi.org//10.1890/08-1680.1

Ruzicka, K. J., Groninger, J. W., & Zaczek, J. J. (2010). Deer Browsing, Forest Edge Effects, and Vegetation Dynamics Following Bottomland Forest Restoration. Restoration Ecology, 18(5), 702–710. doi: https://doi.org//10.1111/j.1526-100X.2008.00503.x

Sage, R. B., Hollins, K., Gregory, C. L., Woodburn, M. I. A., & Carroll, J. P. (2004). Impact of roe deer Capreolus capreolus browsing on understorey vegetation in small farm woodlands. Wildlife Biology, 10(2), 115–120.

Salk, T. T., Frelich, L. E., Sugita, S., Calcote, R., Ferrari, J. B., & Montgomery, R. A. (2011). Poor recruitment is changing the structure and species composition of an old-growth hemlock-hardwood forest. Forest Ecology and Management, 261(11), 1998–2006. doi: https://doi.org//10.1016/j.foreco.2011.02.026

Schippers, P., van Teeffelen, A. J. A., Verboom, J., Vos, C. C., Kramer, K., & WallisDeVries, M. F. (2014). The impact of large herbivores on woodland-grassland dynamics in fragmented landscapes: The role of spatial configuration and disturbance. Ecological Complexity, 17, 20–31. doi: https://doi.org//10.1016/j.ecocom.2013.07.002

Smit, C., Vandenberghe, C., den Ouden, J., & Muller-Scharer, H. (2007). Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. Oecologia, 152(2), 265–273. doi: https://doi.org//10.1007/s00442-006-0650-6

Stritar, M. L., Schweitzer, J. A., Hart, S. C., & Bailey, J. K. (2010). Introduced ungulate herbivore alters soil processes after fire. Biological Invasions, 12(2), 313–324. doi: https://doi.org//10.1007/s10530-009-9624-z

Suzuki, M., & Ito, E. (2014). Combined effects of gap creation and deer exclusion on restoration of belowground systems of secondary woodlands: A field experiment in warm-temperate monsoon Asia. Forest Ecology and Management, 329, 227–236. doi: https://doi.org//10.1016/j.foreco.2014.06.028

Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M., & Kikvidze, Z. (2013). Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. Oikos, 122(1), 104–110. doi: https://doi.org//10.1111/j.1600-0706.2012.20431.x

Tahtinen, B., Murray, B. D., Webster, C. R., Tarasoff, C. S., & Burton, A. J. (2014). Does Ungulate Foraging Behavior in Forest Canopy Gaps Produce a Spatial Subsidy with Cascading Effects on Vegetation? Forest Science, 60(5), 819–829. doi: https://doi.org//10.5849/forsci.13-080

Tanentzap, A. J., Burrows, L. E., Lee, W. G., Nugent, G., Maxwell, J. M., & Coomes, D. A. (2009). Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology, 46(5), 1064–1072. doi: https://doi.org//10.1111/j.1365-2664.2009.01683.x

Tsujino, R., & Yumoto, T. (2004). Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecological Research, 19(3), 291–300. doi: https://doi.org//10.1111/j.1440-1703.2004.00638.x

Tyler, C. M., Davis, F. W., & Mahall, B. E. (2008). The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. Forest Ecology and Management, 255(7), 3063–3074. doi: https://doi.org//10.1016/j.foreco.2008.01.073

Van Hees, A. F. M., Kuiters, A. T., & Slim, P. A. (1996). Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. Forest Ecology and Management, 88(1–2), 55–63. doi: https://doi.org//10.1016/s0378-1127(96)03809-1
Vila, A. R., & Borrelli, L. (2011). Cattle in the Patagonian forests: Feeding ecology in Los Alerces National Reserve. Forest Ecology and Management, 261(7), 1306–1314. doi: https://doi.org//10.1016/j.foreco.2011.01.009
Vila, B., Torre, F., Martin, J. L., & Guibal, F. (2003). Response of young Tsuga heterophylla to deer browsing: developing tools to assess deer impact on forest dynamics. Trees-Structure and Function, 17(6), 547–553. doi: https://doi.org//10.1007/s00468-003-0272-0
Ward, A. I., White, P. C. L., Smith, A., & Critchley, C. H. (2004). Modelling the cost of roe deer browsing damage to forestry. Forest Ecology and Management, 191(1–3), 301–310. doi: https://doi.org//10.1016/j.foreco.2003.12.018
Webster, C. R., Jenkins, M. A., & Rock, J. H. (2005). Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation, 125(3), 297–307. doi: https://doi.org//10.1016/j.biocon.2005.03.027
Welch, D., & Scott, D. (1998). Bark-stripping damage by red deer in a Sitka spruce forest in western Scotland - IV. Survival and performance of wounded trees. Forestry, 71(3), 225–235. doi: https://doi.org//10.1093/forestry/71.3.225
White, M. A. (2012). Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest. Forest Ecology and Management, 269, 222–228. doi: https://doi.org//10.1016/j.foreco.2011.12.043
Willis, J. L., Walters, M. B., & Gottschalk, K. W. (2015). Scarification and gap size have interacting effects on northern temperate seedling establishment. Forest Ecology and Management, 347, 237–246. doi: https://doi.org//10.1016/j.foreco.2015.02.026
Wright, D. M., Tanentzap, A. J., Flores, O., Husheer, S. W., Duncan, R. P., Wiser, S. K., & Coomes, D. A. (2012). Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. Biological Conservation, 153, 64–71. doi: https://doi.org//10.1016/j.biocon.2012.04.033

## References

Alverson, W.S., Waller, D.M., Solheim, S.L., 1988. Forests too deer: edge effects in northern Wisconsin. Conserv. Biol. 2, 348–358.
Augustin, N.H., Cummins, R.P., French, D.D., 2001. Exploring spatial vegetation dynamics using logistic regression and a multinomial logit model. J. Appl. Ecol. 38, 991–1006.
Augustine, D.J., Frelich, L.E., 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. 12, 995–1004.
Bruinderink, G., Hazebroek, E., 1996. Wild boar (Sus scrofa scrofa L.) rooting and forest regeneration on podzolic soils in the Netherlands. For. Ecol. Manage. 88, 71–80.
Brullhardt, M., Risch, A.C., Filli, F., Haller, R.M., Schutz, M., 2015. Spatiotemporal dynamics of natural tree regeneration in unmanaged subalpine conifer forests with high wild ungulate densities. Can. J. For. Res. 45, 607–614.
Clutton-Brock, T.H., Coulson, T., Milner, J.M., 2004. Red deer stocks in the highlands of Scotland. Nature 429, 261–262.
Cook, R.C., Cook, J.G., Irwin, L.L., 2003. Estimating elk body mass using chest-girth circumference. Wildlife Soc. Bull. 536–543.
Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Ann. Rev. Ecol., Evolut., Syst. 113–147.
Cromsigt, J.P., Kuijper, D.P., 2011. Revisiting the browsing lawn concept: evolutionary interactions or pruning herbivores? Perspect. Plant Ecol., Evolut. Syst. 13, 207–215.
Cromsigt, J.P., Kuijper, D.P., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I., Mysterud, A., Schmidt, K., West, K., 2013. Hunting for fear: innovating management of human–wildlife conflicts. J. Appl. Ecol. 50, 544–549.
De Jong, C., Gill, R., Van Wieren, S., Burlton, F., 1995. Diet selection by roe deer Capreolus capreolus in Kielder Forest in relation to plant cover. For. Ecol. Manage. 79, 91–97.
Eycott, A.E., Watkinson, A.R., Hemami, M.R., Dolman, P.M., 2007. The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. Oecologia 154, 107–118.
Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Ann. Rev. Ecol., Evolut., Syst. 557–581.
Fuller, R.J., Gill, R.M., 2001. Ecological impacts of increasing numbers of deer in British woodland. Forestry 74, 193–199.
Garcia-Gonzalez, R., Cuartas, P., 1996. Trophic utilization of a montane/subalpine forest by chamois (Rupicapra pyrenaica) in the Central Pyrenees. For. Ecol. Manage. 88, 15–23.
Genov, P.V., Massei, G., 2004. The environmental impact of wild boar. Galemys: Boletín informativo de la Sociedad Española para la conservación y estudio de los mamíferos 16, 135–145.
Gill, R., Morgan, G., 2010. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. Forestry 83, 53–63.
Glutton-Brock, T., Albon, S., 1992. Trial and error in the Highlands. Nature 358, 11–12.
Gordon, I.J., Prins, H.H., 2008. Introduction: Grazers and Browsers in a Changing World. Springer.
Heckel, C.D., Bourg, N.A., McShea, W.J., Kalisz, S., 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. Ecology 91, 319–326.
Hefley, T.J., Hygnstrom, S.E., Gilsdorf, J.M., Clements, G.M., Clements, M.J., Tyre, A.J., Baasch, D.M., VerCauteren, K.C., 2013. Effects of deer density and land use on mass of white-tailed deer. J. Fish Wildlife Manage. 4, 20–32.
Holloway, C.W., 1967. The effect of red deer and other animals on naturally regenerated Scots pine. University of Aberdeen (United Kingdom).
Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118.
Kleiber, M., 1947. Body size and metabolic rate. Physiol. rev 27, 511–541.
Kuiters, A., Mohren, G., Van Wieren, S., 1996. Ungulates in temperate forest ecosystems. For. Ecol. Manage. 88, 1–5.
Lindroth, R.L., St. Clair, S.B., 2013. Adaptations of quaking aspen (Populus tremuloides Michx.) for defense against herbivores. For. Ecol. Manage. 299, 14–21.
Lott, D.F., Galland, J.C., 1987. Body mass as a factor influencing dominance status in American bison cows. J. Mammal. 68, 683–685.
Lucas, R.W., Salguero-Gomez, R., Cobb, D.B., Waring, B.G., Anderson, F., McShea, W.J., Casper, B.B., 2013. White-tailed deer (Odocoileus virginianus) positively affect the growth of mature northern red oak (Quercus rubra) trees. Ecosphere 4, 15.
Merino, M.L., Milne, N., Vizcaíno, S.F., 2005. A cranial morphometric study of deer (Mammalia, Cervidae) from Argentina using three-dimensional landmarks. Acta Theriol. 50, 91–108.
Motta, R., 2003. Ungulate impact on rowan (Sorbus aucuparia L.) and Norway spruce (Picea abies (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. For. Ecol. Manage. 181, 139–150.
Murray, B.D., Webster, C.R., Bump, J.K., 2014. A migratory ungulate facilitates cross-boundary nitrogen transport in forested landscapes. Ecosystems 17, 1002–1013.
Nuttle, T., Ristau, T.E., Royo, A.A., 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. J. Ecol. 102, 221–228.
Parker, K.L., Gillingham, M.P., Hanley, T.A., Robbins, C.T., 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (Odocoileus hemionus sitkensis) in Alaska. Can. J. Zool. 71, 1397–1404.
Pellerin, M., Said, S., Richard, E., Hamann, J.-L., Dubois-Coli, C., Hum, P., 2010. Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. For. Ecol. Manage. 260, 429–437.
Prins, H.H., Fritz, H., 2008. Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. The Ecology of Browsing and Grazing. Springer, pp. 179–200.
Putman, R., Langbein, J., Green, P., Watson, P., 2011. Identifying threshold densities for wild deer in the UK above which negative impacts may occur. Mammal Rev. 41, 175–196.
Reimoser, F., 2003. Steering the impacts of ungulates on temperate forests. J. Nat. Conserv. 10, 243–252.
Reimoser, F., Putman, R., 2011. Impacts of wild ungulates on vegetation: costs and benefits. Ungulate Management in Europe: Problems and Practices. Cambridge University Press, Cambridge, pp. 144–191.
Renaud, P., Verheyden-Tixier, H., Dumont, B., 2003. Damage to saplings by red deer (Cervus elaphus): effect of foliage height and structure. For. Ecol. Manage. 181, 31–37.
Rooney, T.P., 2001. Deer impacts on forest ecosystems: a North American perspective. Forestry 74, 201–208.
Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manage. 181, 165–176.
Rowcliffe, M.J., Carbone, C., Jansen, P.A., Kays, R., Kranstauber, B., 2011. Quantifying the sensitivity of camera traps: an adapted distance sampling approach. Methods Ecol. Evol. 2, 464–476.
Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.
Schippers, P., van Teeffelen, A.J.A., Verboom, J., Vos, C.C., Kramer, K., WallisDeVries, M.F., 2014. The impact of large herbivores on woodland-grassland dynamics in fragmented landscapes: the role of spatial configuration and disturbance. Ecol. Complex. 17, 20–31.
Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., Hiraldo, F., 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. Ann. Rev. Ecol., Evolut., Syst. 1–19.

Stephenson, T.R., Hundertmark, K.J., Schwartz, C.C., Ballenberghe, V.V., 1998. Predicting body fat and body mass in moose with ultrasonography. Can. J. Zool. 76, 717–722.
Suzuki, M., Onuma, M., Yokoyama, M., Kaji, K., Yamanaka, M., Ohtaishi, N., 2001. Body size, sexual dimorphism, and seasonal mass fluctuations in a larger sika deer subspecies, the Hokkaido sika deer (Cervus nippon yesoensis Heude, 1884). Can. J. Zool. 79, 154–159.
Svenning, J.-C., Pedersen, P.B., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.M., Sandel, B., Sandom, C.J., Terborgh, J.W., 2015. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proc. Nat. Acad. Sci. 201502556.
Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923–1926.
Tilghman, N.G., 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildlife Manage. 524–532.
Tyler, C.M., Davis, F.W., Mahall, B.E., 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. For. Ecol. Manage. 255, 3063–3074.
Van Hees, A.F.M., Kuiters, A.T., Slim, P.A., 1996. Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. For. Ecol. Manage. 88, 55–63.
Welch, D., Scott, D., 1998. Bark-stripping damage by red deer in a Sitka spruce forest in western Scotland – IV. Survival and performance of wounded trees. Forestry 71, 225–235.