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

Authors

J. Ignacio Ramirez[1,2]; Patrick A. Jansen[2,3]; Jan den Ouden[1]; Leo Goudzwaard[1]; Lourens Poorter[1]

Author Affiliation

Forest Ecology and Forest Management Group, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, the Netherlands.

Resource Ecology Group, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, the Netherlands.

Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Balboa, Ancon, Panama.

Corresponding Author

Juan Ignacio Ramirez – juanignacio.ramirez@icloud.com

Forest Ecology and Forest Management Group, Department of Environmental Sciences, Wageningen University & Research, P. O. Box 47, 6700 AA Wageningen, The Netherlands.

Abstract

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

Abbreviations

PCA= Principal Component Analysis; GLMM =Generalized Linear Mixed Models

Keywords

Ungulates; Browsing; Diversity; Structure; Functioning; Forest; Temperate; Succession.

1. Introduction

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

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

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

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

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

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

2. Methods

2.1. Study area

The Veluwe is located in the central part of the Netherlands with a total extension of 1200 km². Annual average precipitation is 900 mm yr^{-1}, whereas the annual average temperature is 9.4°C, with monthly temperature means ranging from 2.5°C in January to 16.4°C in July (Kuiters & Slim 2002). The main soil types consist of xeric humic podzols and brown earths (inceptisols), depending on the parent material that range from aeolic drift and cover sands to Pleistocene loamy fluvioglacial sands (Kuiters & Slim 2002). The Veluwe is covered by a mosaic of forests, drift sands and heathland, where forests cover two thirds of the total area. The main species are *Pinus sylvestris, Quercus robur, Fagus* *sylvatica, Larix kaempferi, Pseudotsuga menziesii* and *Betula pendula*. Although ungulate assemblage varies across the Veluwe, the main species are roe deer (*Capreolus capreolus),* fallow deer *(Dama dama),* red deer *(Cervus elaphus)* and wild boar *(Sus scrofa),* with an average density of 13.6 animals per km^{-2} in 1998 (Kuiters & Slim 2002) and considerable increase during the last decades. Forest managers in this area generally aim to transform even-aged single coniferous species into mixed forest stands, and create small clearings to stimulate natural regeneration of a mix of native species.

2.2. Study design

To assess the effects of wild ungulates on long-term forest succession, we compiled a set of existing fenced plots that were established in recent clear cuts to protect forest regeneration from ungulates, paired with neighbouring unfenced plots, that were ca. 10 m apart. In total, we identified 27 fenced and unfenced plots in 17 different forest sites with plots ranging in age from 1 to 33 years since establishment. Plot size varied from 0.01 to 0.75 ha, and the number of pairs per site varied from 1 to 6 (Appendix A.1*)*. We surveyed the vegetation during the late summer of 2016 and 2017. Within each pair of fenced/unfenced plots, 5x5 m quadrats were randomly established by drawing numbers for the x and y axis, which represented a coordinate system. We established two quadrats per plot when regeneration heterogeneity was low (i.e., low species diversity and little variation in forest structure), and three or four quadrats per plot when heterogeneity was high. Data from all quadrats were averaged to obtain values for a plot.

2.3. Response variables

We quantified 15 response variables that are commonly used in studies into ungulate-forest interactions. Each variable was then averaged across all 5x5 m quadrats within treatments for each of the 17 forest sites. Eleven response variables were used to describe forest structure: stem density of trees 0.1-0.49 m height, 0.5-4.99 m height, and 5-30 m height, total understory vegetation cover, heath (heather and *Ulex*) cover, fern (*Polypodiopsida* and *Pteridium*) cover, shrub cover (bramble (*Rubus spp.)* and woody shrub species), moss (*Bryophyta*) cover, grass (*Gramineae*) cover, non-living "other" (branches, litter and exposed soil) cover and canopy (overstory) cover. Heath was recorded separate to shrub cover because this type of vegetation is quite common in Dutch forests. Three variables were used to describe forest composition: species richness, Shannon diversity and proportion of coniferous trees in the vegetation. Finally, litter depth was measured. Only woody plants >10 cm in height were measured, as smaller recent germinants show large fluctuations in population size.

Each woody individual was identified, its height measured as the vertical distance between the forest floor and the apex and browsing damage was quantified as the presence (coded as 1) or absence (coded as 0) of damaged branches and leaves on any part of the plant, independent of the number of browsed leave sort branches. Canopy cover, which determines understory light availability, was measured in each quadrat with a spherical densitometer, taking one reading per cardinal direction (Millington et al. 2011). The dominant canopy tree species determine to certain extend the type of canopy cover (sparse or closed) and have a large effect on the composition of the local seed rain (Gill & Beardall 2001). We identified therefore the two species with the highest abundance in the canopy of the residual forest. Because understory vegetation competes directly for light and nutrients with tree seedlings and saplings (Naaf & Wulf 2007) we estimated understory vegetation cover by determining, with the use of a grid (1x1 m), the cover percentage of the different vegetation types (heath, fern, shrub, moss, grass and non-living) up to 1.5 m height for each quadrat. Litter depth represents the amount of un-fragmented and fragmented litter layer, which is available for decomposition. Litter depth also acts as a barrier for the establishment of species in the seedbank (Facelli & Pickett 1991; Schramm & Ehrenfeld 2010). We quantified litter depth at two points per quadrat, by measuring the thickness of the litter layer with a ruler, then we averaged the values for the entire plot.

Stem density was quantified as the average number of trees per square meter. Stem density was than categorized in three classes: stem density for individuals with a height ranging from 0.1 to 0.49 m (saplings), from 0.5 to 4.99 m (poles) and from 5 to 30 m (trees) to differentiate between the different developmental stages of trees.

To evaluate the effect of ungulates on forest understory (< 1.5 m height), vegetation cover was visually quantified as the projected cover area of different understory vegetation on the forest floor (expressed as cover percentage, varying from 0% to 100%). Vegetation cover was then subdivided in five categories heath, fern, shrub, moss, grass and other, all together add up to 100%. Species richness was quantified by the average number of tree species per plot. Shannon diversity was calculated as:

$$H' = -\sum_{i=1}^{s} p_i * \ln(p_i)$$

where (p_i) is the proportion of individuals of one particular species found relative to all individuals, (ln) is the natural log, ($\sum$) is the sum of the calculation and (s) is the number of species. The conifer proportion (Cp) was calculated as:

$$Cp = \frac{C}{C+B}$$

where (C) is the number of conifer individuals and (B) is the number of broadleaved individuals. Litter depth was calculated as the average height of the litter layer. Finally, forest type was determined by the canopy tree composition index that highlight the monodominance of the forest stand. If dominant and subdominant trees were broadleaved from the same species it was assigned a code of 1, if the canopy was composed of two different broadleaved species 0.75 was assigned, if the canopy consisted of one broadleaved and one conifer species 0.5 was assigned, if the canopy consisted only of two different conifer species 0.25 was assigned and if the canopy was composed of conifer species of the same species 0 was assigned.

2.4. Statistical analysis

To test the three predictions of ungulate impacts on vegetation characteristics, we used a series of Generalized Linear Mixed Models (GLMM), with ungulate treatment (fenced vs unfenced), time since establishment and forest type as fixed factors and forest site (i.e., the 17 forests) as a random grouping factor. We also included current ungulate abundance as fixed factors because ungulate historical records were not available, but the results were not significant, thus it was excluded from the analysis. The ungulate data was gathered using camera traps during summer and autumn of 2017. Abundance ranged from 2 to 102 ungulates trapped per 100 camera-days, with an average of 25 ungulates per 100 camera-days across all sites (corresponding to an average of 20 *Sus scrofa*, 3 *Cervus elaphus,* 2 *Capreolus capreolus* and 0 *Dama dama*). Because response variables typically show a nonlinear, saturating relationship over age, with rapid changes just after disturbance and slow changes as the stand closes, we $\log_{10}$-transformed age. To test the fourth prediction that ungulate browsing leads towards an arrested early-successional vegetation, dominated by light demanding species, we used an unconstrained Principal Component Analysis (PCA) (Borcard et al. 2018) with the abundance of 13 species as response variables (*Amelanchier lamarckii, Betula pendula, Betula pubescens, Castanea sativa, Fagus sylvatica, Larix kaempferi, Pinus sylvestris, Prunus serotina, Pseudotsuga menziesii, Quercus robur, Quercus rubra, Rhamnus frangula* and *Sorbus aucuparia*), six understory vegetation cover variables (fern, shrub, moss, grass, *Vaccinium* and "other"), two stand variables (light and canopy) and three treatment variables (age, fenced and unfenced). For all statistical analyses, R (R Core Team 2017) was used in combination with "nlme" and "stats" packages (Pinheiro et al. 2014; R Core Team 2017)

3. Results

3.1. Forest structure

None of the forest structure attributes differed between treatments (fenced or unfenced). Two of the eleven variables evaluated varied significantly over age, or showed an age-treatment interaction (understory vegetation cover and canopy cover. Table 1). Canopy cover increased overage, more strongly so for the fenced than for the unfenced plots (the slope for the fenced plots is β=63.8, unfenced β=42, please note that age has been $\log_{10}$-transformed, Fig. 1K). Understory cover increased with age for the unfenced plots but it decreased with age for the fenced plots (unfenced β=6.1, fenced β=-14.9, Fig. 1D).

3.2. Forest composition

The response variables related to forest composition did not differ significantly between treatments. Nevertheless, age and age-treatment interaction had a significant effect on species richness and Shannon diversity. Thus, species richness decreased with age in the unfenced plots but not in the fenced plots (unfenced β=-2.5, fenced β=-0.6, Fig. 1L). Shannon diversity also decreased with age in the unfenced plots but not in the fenced plots (unfenced β=-0.6, fenced β =-0.1, Fig. 1M). Browsing intensity was highest for *Sorbus* *aucuparia (88% of the individuals, Fig. 2) followed by Rhamnus frangula (*86%), *Amelanchier lamarckii (*85%), *Quercus robur (*77%), *Betula pendula (*48%*)*, *Larix kaempferi (*21%*)*, *Pinus sylvestris (*20%), *Quercus petrea (*8%) and *Pseudotsuga menziesii (*0%).

3.3. Forest litter depth

Litter depth differed significantly between treatments. Litter depth increased with age on the fenced plots but decreased with age on the unfenced plots (fenced β=2.8, unfenced β=-0.4, Fig. 1O).

Table 1. Mixed linear model fits for the effects of exposure to ungulates on 15 aspects from vegetation development in 17 forest clearings on poor sandy soils at the Veluwe, the Netherlands (n=27 plots). For each component: units and the coefficient of determination (R^2) is given as well as the coefficients of age since vegetation development, treatment (i.e., fenced vs. unfenced), interaction (age and treatment) and forest type (when the forest canopy is composed only by a single conifer species is coded as 0 and 1 for a single broadleaved species and values in between represent a mix of tree species) are given. The slope of fenced and unfenced plots is calculated based only on the coefficients of age (log_{10} Age), treatment and interaction. All models were fitted with 3 degrees of freedom. Significant coefficients are indicated by an asterisk.

		Slope			Coefficients			
Component	**Units**	**Unfenced**	**Fenced**	**R²**	**Age**	**Treatment**	**Interaction**	**Forest type**
Structure								
Density saplings	Stems/m²	-0,6	-0,5	0,49	-0,6	-0,1	0,1	0,2
Density poles	Stems/m²	-0,3	1,2	0,26	-0,3	-0,4	1,5	2,4
Density trees	Stems/m²	0,1	0,2	0,37	0,1	-0,1	0,1	-0,3
Und. Veg. cover	%	6,1	-14,9	0,49	6,1	1,6	-21*	-9,6
Heath cover	%	5,4	-10,8	0,73	5,4	3,2	-16,2	-29,2
Fern cover	%	5,4	-1,3	0,18	5,4	3,6	-6,7	-0,9
Shrub cover	%	29,2	14,6	0,39	29,2	8,1	-14,6	49,3
Moss cover	%	-4,1	6,2	0,23	-4,1	2,7	10,3	-34,9
Grass cover	%	-31,2	-17,3	0,44	-31,2	-20,6	13,9	-7,4
Other cover	%	-6,4	7,0	0,4	-6,4	3,0	13,4	6,5
Canopy cover	%	*42,0*	63,8	0,83	42,0**	-0,3	21,9**	-26,2
Composition								

Richness	Species	*-2,5*	-0,6	0,66	-2,5**	0,1	1,9*	-2,8
Shannon diversity	Index	-0,6	-0,1	0,94	-0,6*	<0,1	0,5*	-0,7
Conifer proportion	Index	-0,1	-0,2	0,41	-0,1	<0,1	-0,1	0,6
Functioning								
Litter depth	cm	0,4	2,8	0,85	0,4	0,1	2,3**	1,28

** p-value between 0.01<x<0.05, ** p-value <0.01.*

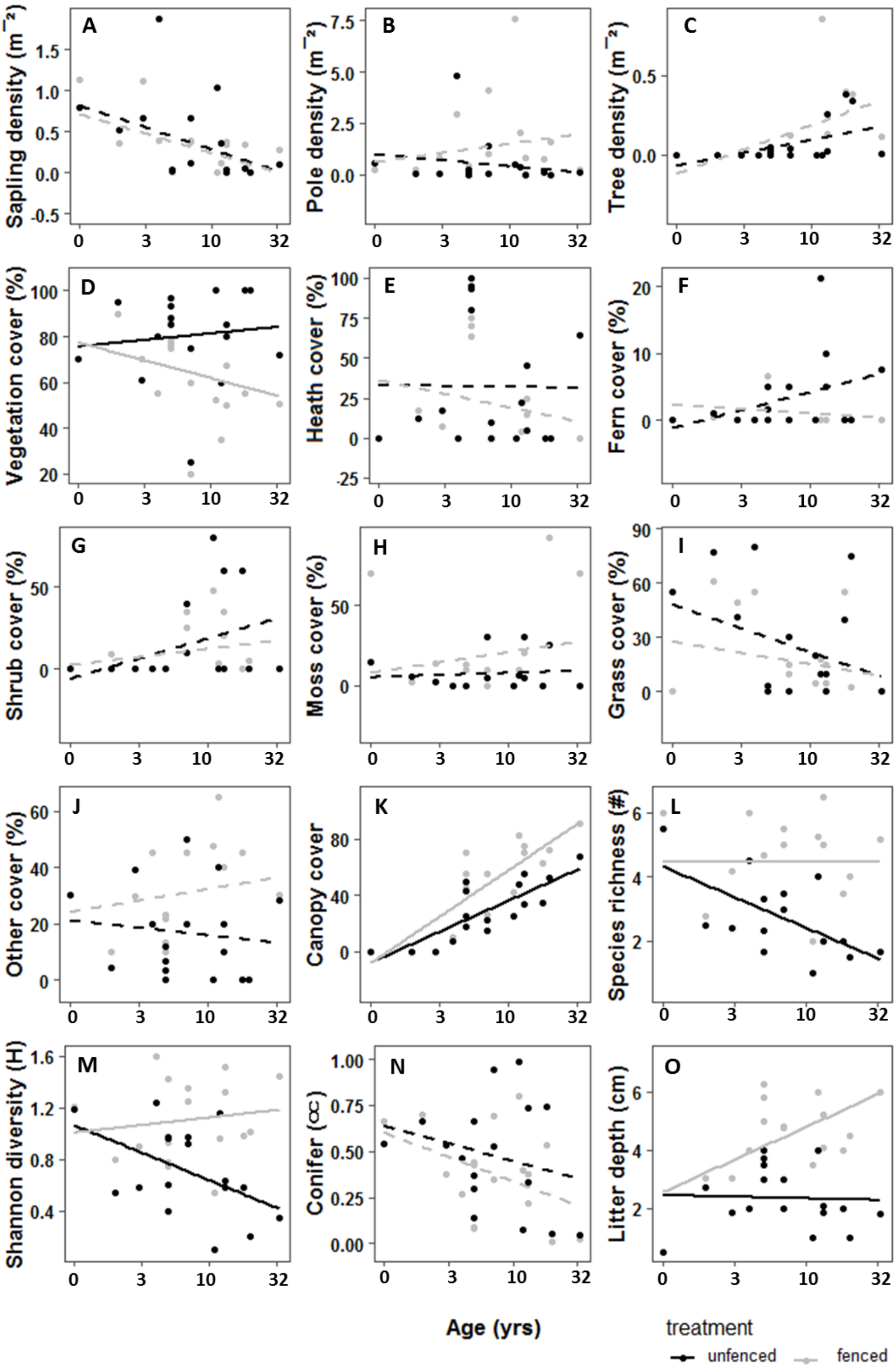

Figure 1. Effects of exposure to ungulates (i.e.,17 fenced and 17 unfenced plots) on vegetation development over age in forest clearings on poor sandy soils at the Veluwe, the Netherlands. Plots compare 15 vegetation characteristics between fenced and unfenced plots of different age. Lines are simple linear regression fits (independent variables=age:treatment and response variables) for unfenced (black) and fenced (gray) plots. Each pannel has a letter assigned in upper left corner, solid lines indicate significance in the model whereas dashed lines are non-significant.

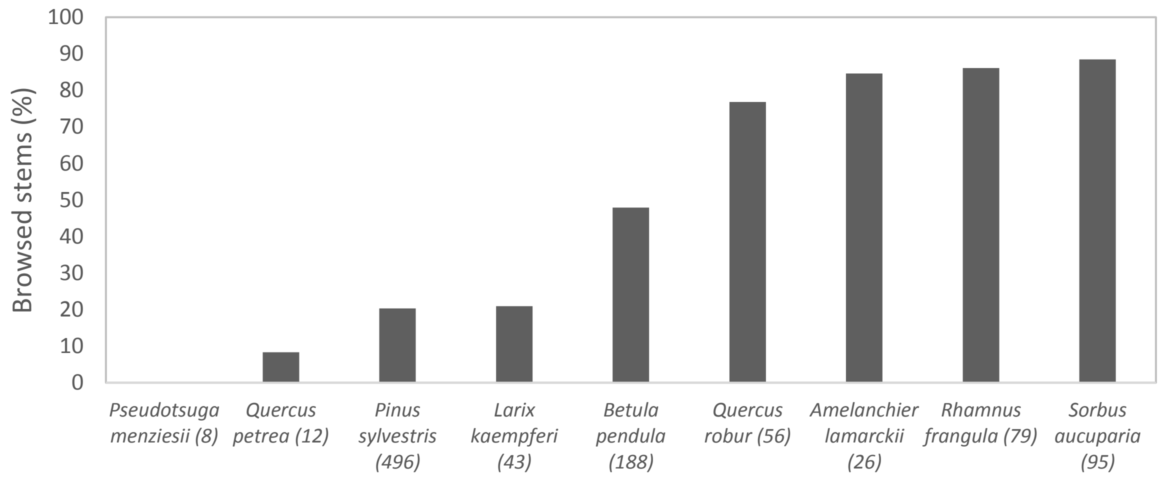

Figure 2. Percentage of browsed stems for main species present (>7 individuals) across all unfenced quadrats (25 m²) in the Veluwe, the Netherlands. The number of replicate stems are shown in parenthesis. Browsing intensity differed significantly among species (Kruskal-Wallis test, x^2=316, df=8, p<0.000).

3.4. Forest succession

The first two component axes of the PCA explained 34.3% of the variation in species composition (Fig. 3). On the PCA ordination biplot a diagonal axis from upper left (fenced plots), to lower right (unfenced plots) is perceived. High abundance of *Betula pendula, Prunus serotina, Quercus robur, Betula pubescens* and shrubs is largely associated with fenced plots and low abundance of these species was associated with unfenced plots. No species was particularly abundant in unfenced plots. A second axis from lower left (canopy cover) to upper right (light availability) is perceived. *Fagus sylvatica, Castanea sativa, Pseudotsuga menziesii* and moss are largely associated with time and canopy cover, whereas *Sorbus aucuparia, Rhamnus frangula, Amelanchier lamarckii* and grass are associated with high light availability.

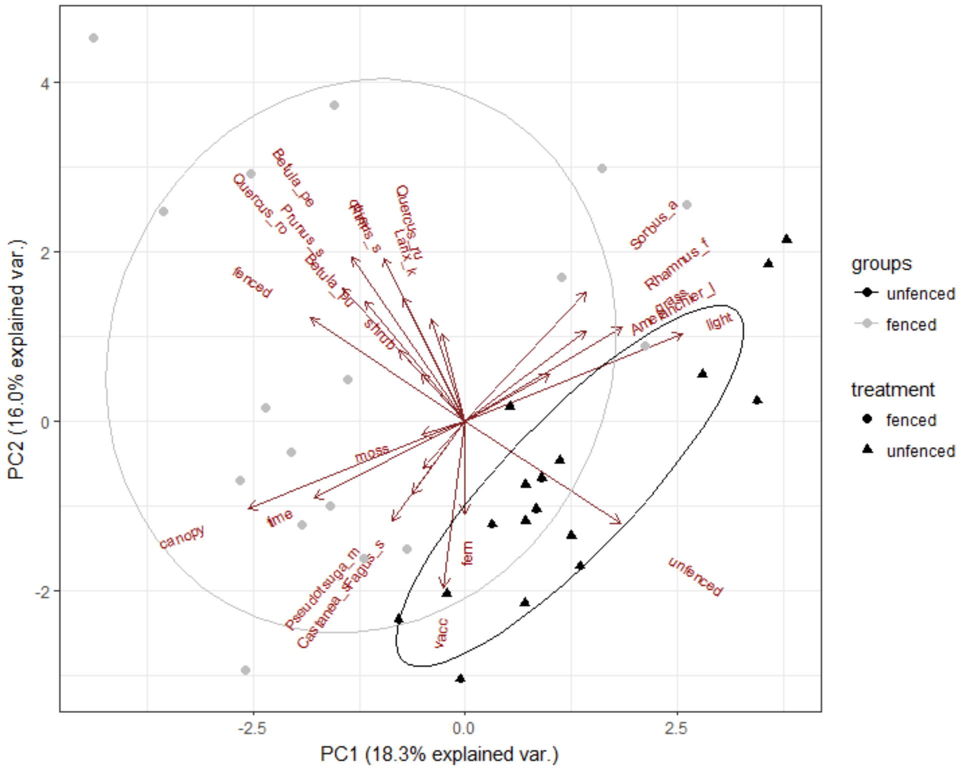

Fig. 3. Results of a Principal Components Analysis (PCA) of forest structure, composition and functioning of 17 fenced (grey circles) and 17 unfenced (black triangles) plots with different age since vegetation development in forest clearing. The plots were established on poor sandy soils at the Veluwe, the Netherlands and all woody plants > 10 cm height were included. The length of the arrow is proportional to its importance and the angle between two arrows reflects the magnitude of the correlation between variables. Principal Component Axis 1 (PC 1) explains 18.3% of variation and PC2 explains 16% of the variation. The ellipses indicate the confidence region of fenced and unfenced plots in the plane. Variables are coded as follows: time=age, fenced=fenced, unfenced=unfenced, vacc=Vaccinium, fern=fern, shrub=shrub, moss=moss, grass=grass, other=non-living, canopy=canopy cover, light=light availability, Amelanchier_l=Amelanchier lamarckii, Betula_pe=Betula pendula, Betula_pu=Betula pubescens, Castanea_s=Castanea sativa, Fagus_s=Fagus sylvatica, Larix_k=Larix kaempferi, Pinus_s=Pinus sylvestris, Prunus_s=Prunus serotina, Pseudotsuga_m=Pseudotsuga menziesii, Quercus_ro=Quercus robur, Quercus_ru=Quercus rubra, Rhamnus_f=Rhamnus frangula, Sorbus_a=Sorbus aucuparia.

4. Discussion

We used a chronosequence of ungulate exclosure experiments to assess the long-term effects of ungulates on tree recruitment and forest regrowth in forest clearings on poor sandy soils in the Netherlands. Our results indicate that ungulates steer succession by reducing species diversity and litter accumulation, and by shifting forest structure and species composition, where palatable species such as *Betula pendula and Quercus robur* are favoured by fencing, shade-tolerant species such *as Pseudotsuga menziesii, Castanea sativa* and *Fagus sylvatica* were unaffected by ungulate fencing, but influenced by time.

4.1. Forest structure

We predicted that browsing by ungulates would reduce canopy and understory vegetation cover. In the unfenced plots, presence of ungulates indeed led to a slower closure of the canopy (Fig. 1K), which resulted in reduced shading and an increased understory vegetation cover (Fig. 1D). Similarly, in Japanese temperate forest, browsing and stripping by sika deer reduced the number of trees reaching the forest canopy, resulting in a more open forest stand (Akashi & Nakashizuka 1999). Other studies also found that ungulates can promote grasses, ferns and sedges in open and thinned forest stands (Gill 1992; Horsley et al. 2003) by removing competing trees and increasing light availability on the forest floor, although grasses and sedges can compete with tree seedlings by inhibiting their establishment (Gill 1992).

Our finding that ungulates did not decrease sapling density (Fig. 1A) disagrees with several previous studies that found that ungulates reduce stem density by actively browsing on forest regeneration, leading to an open understory over time (Putman et al. 1989; Klopcic et al. 2010; Salk et al. 2011; Ramirez et al. 2018). Our result can be explained by the fact that forest in fenced plots had mature and young trees, which form several forest layers and a denser canopy cover that limited the amount of light reaching the understory, meaning that little regeneration establishes and develops under these circumstances (Whitmore 1989). Ungulates did not have a significant effect on the density of trees in larger size classes (Fig. 1B and C), probably because at this stage trees are robust enough to tolerate browsing, or tall enough (e.g., >2 meters) to escape browsing (Rooney 2001;

Lindroth & Clair 2013). Yet, we do not know if they reduce the overall foliage of trees, which can result in a lower canopy cover (Fig. 1k).

4.2. Forest composition

We predicted that ungulates steer forest composition by reducing the richness and diversity of regenerating trees by selectively browsing on palatable broadleaved trees (Rooney & Waller 2003), which leads to competitive release of conifers. Species richness and Shannon diversity indeed decreased rapidly over time in unfenced plots where ungulates were present (Fig. 1L and M). Our findings are in line with other studies, where the floristic composition and richness of mixed forests (Hedl et al. 2010) and understory diversity (McShea & Rappole 2000; Ramirez et al. 2018) decreased with the continued presence of ungulates. In fenced plots, there was no passive accumulation of species over time, but rather a constant richness and diversity because of shading, probably due to the dominance of the shade-tolerant climax species, *Fagus sylvatica*.

We predicted that ungulate browsing leads to an increase in the proportion of conifer trees in the regeneration. Yet, the proportion of coniferous trees did not vary between fenced and unfenced plots (Fig. 1N). Similarly, (McGarvey et al. 2013), did not find a general effect of browsing on tree species composition. There are two potential explanations for this result. First, the composition of seed trees in the surrounding mature forest determines the species composition of the forest understory (Gill & Beardall 2001) regardless of successional stage. However, the results of our GLMM, indicate that forest type did not have a significant effect in any of the forest components (Table 1). Second, ungulate density was not sufficiently high to trigger such effects. For instance, in a global temperate forest meta-analysis, it is shown that an ungulate density >10-23 roe deer per km^{-2} or other similar sized ungulates may affect regeneration establishment, forest structure and succession (Ramirez et al. 2018), whereas in our forests the average density was a bit lower (13.6 ungulates km^{-2}).

4.3. Forest litter depth

We predicted that ungulates can either reduce litter depth on the forest floor by removing a large amount of litter from the floor (Hobbs 1996) and by changing the species composition of the stand to evergreen coniferous species that have a lower litter production rate (Husheer et al. 2005); or increase the litter depth by shifting species composition toward conifers which have more recalcitrant leaves, resulting in an accumulation of litter over time. We indeed found that litter depth increased over time in fenced plots where ungulates were excluded, whereas in the unfenced plots the litter layer depth was lower and constant (Fig. 1O). This means that the trade-off between litter quantity and quality in our system is mainly dominated by litter quantity. A reduction in litter depth by ungulates can have cascading effects on soil invertebrates as it may reduce food availability for invertebrates (Allombert et al. 2005) and leads to a harsher microenvironment with increased soil erosion, irradiance and temperature and a reduced soil humidity.

4.4. Forest succession

We predicted that ungulates steer tree species composition and forest succession by preferentially feeding on palatable species, such as *Sorbus aucuparia, Rhamnus frangula, Amelanchier lamarckii, Quercus robur* and *Betula pendula* (Fig. 2). As expected palatable species such as *Betula pendula, Prunus serotina, Quercus robur, Betula pubescens* and shrubs were strongly associated with fenced plots and had a low abundance in unfenced plots, whereas no specific species were associated with unfenced plots (Fig. 3, Appendix A.3). In circumstances of low food availability, ungulates may even browse on less palatable species until all resources are depleted. This is the reason why no palatable and less palatable species were associated with unfenced plots (Kuiters et al. 1996; Fuller & Gill 2001). Exclusion of ungulates from forest stands thus promotes the establishment and development of palatable species.

We hypothesized that forest succession is a major driver that shifts species composition in forest stands from light-demanding to shade-tolerant species. Because in the course of forest development the formation of a forest canopy limits the amount of light reaching the understory (Alverson et al. 1988). Our prediction was confirmed because small-statured shrubs and treelets such as the intermediate shade tolerant *Sorbus aucuparia, Rhamnus frangula* , grasses and the generalist shrub *Amelanchier lamarckii* (Niinemets & Valladares 2006) were strongly associated with an early successional stage, characterized by light. In contrast, shade tolerant (sub)canopy species such as: *Fagus sylvatica, Castanea sativa, Pseudotsuga menziesii* and the moss layer were strongly associated with later successional stage, characterized by higher canopy cover and deep shade.

This study is one of few studies that evaluated the long-term effects of ungulates on the development of European temperate and boreal forests (Scott et al. 2009; Klopcic et al. 2010; Biuw et al. 2014). All three other studies also found that ungulates altered forest structure, regeneration composition and recruitment within a time frame of approximately 25 years. We used a chronosequence approach, for which we paired fenced plots and unfenced plots in clearings of different age. Although all of our experimental sites belong to the same region, with similar abiotic and biotic conditions, an important limitation remains that it is impossible to control for all variables. In particular, local ungulate abundance will have differed between sites and over time. Our results give a first impression what the long-term effects of ungulates could be. Yet, to really assess these long-term effects it is necessary to use a longitudinal approach which monitors the same plots over a longer period of time.

According to the intermediate disturbance hypothesis, which states that species diversity and ecological functions are maximized when disturbance levels are intermediate (Connell 1978; Wilkinson 1999), ungulates by browsing and trampling can create opportunities for both early and late successional plant species to coexist and thus maximize species diversity. However, our results do not provide evidence that ungulates have positive effects on the different forest attributes besides understory vegetation cover. This can be explained by the relatively high ungulate density (13.6 ungulates km^{-2}) in combination with the low primary productivity of this area. Due to low resource availability, on poor sandy soils, tree saplings cannot resist, tolerate or escape ungulate browsing (Lindroth & St. Clair 2013), especially at a high browsing incidence.

4.5. Recommendations

Ungulates fulfil many functions in the forest such as seed dispersal, increase forest structure heterogeneity through browsing and enhance nutrient cycling in soil by defecation. However, a supra-optimal ungulate density may impair forest regeneration (Van Hees et al. 1996; Pellerin et al. 2010b) and diversity (Fig. 1L & M). In an earlier study at global scale, we found that ungulate densities between 10 and 13 roe deer individuals per km^{-2}, can impair forest recruitment, although critical threshold for densities vary and can be higher for more productive systems (Ramirez et al. 2018). In an earlier study at global scale, we found that ungulate densities between 10 and 13 roe deer individuals per km^{-2}, can impair forest recruitment, although critical threshold for densities vary and can be higher for more productive systems (Ramirez et al. 2018). Once ungulates are removed or introduced to a forest system it is very unlikely that the forest structure and composition will change back to its original state.

In case forest managers would like to bring the system back to the previous conditions, they can exclude ungulates by using exclosures at different temporal and spatial scales, or they can control ungulate populations by reintroducing top predators, modifying forest edge to increase high-quality foliage(Miyashita et al. 2008), providing alternative foliage for ungulates, and/or by adaptively controlling the number of reproductive female ungulates through lethal or non-lethal management strategies (Augustine & Frelich 1998; Clutton-Brock et al. 2004; Sergio et al. 2008; Reimoser & Putman 2011).

5. Conclusions

In this temperate forest system, on sandy soils, ungulates had moderate long-term effects on forest structure, composition and succession. Ungulates significantly affected 38% of the 16 variables evaluated, by reducing canopy cover, species richness, Shannon diversity and litter depth, increasing understory vegetation cover and changing species composition. All the other variables had a high resilience to ungulates; they had either high resistance against browsing or a high recovery after browsing. Nevertheless, browsing by ungulates can eventually slow down regular forest succession that proceeds from light demanding species to shade tolerant species by keeping the system in an arrested state composed mainly of light demanding species. These effects can ultimately cascade to the entire ecological community.

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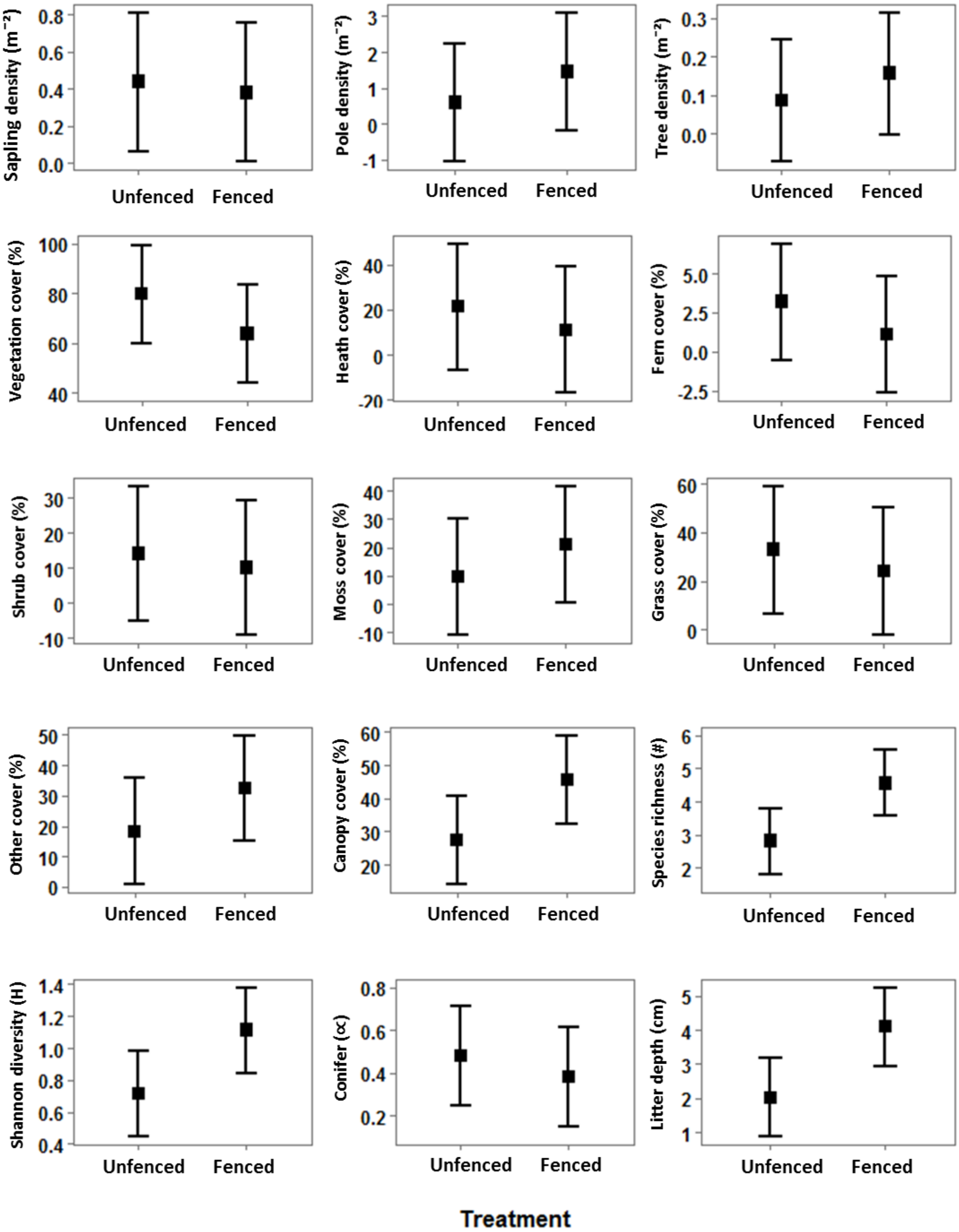
Appendix A.

A.1. List of plots included in this study. Forest site refers to the location of the fenced/unfenced plots. Year refers to the plot establishment date and time indicates the years since establishment. Replicates specify the number of fenced/unfenced plots in each forest site. Quadrat refers to the number of vegetation plots measured. The size of all quadrats is of 25 m².

Forest site	Establishment (yr)	Age (yrs)	Replicates	Quadrats per plot	GPS coordinates
Oostereng	2016	1	1	2	51°59'09.9"N 5°42'59.3"E
Veluwe S.	2015	2	5	2	52°03'15.8"N 5°50'47.5"E
Veluwe N.	2014	3	6	2	52°07'01.8"N 5°50'05.7"E
Rheden	2013	4	1	3	52°01'15.2"N 5°59'02.0"E
Achterpark N.	2012	5	1	3	52°13'44.3"N 5°54'27.6"E
Achterpark S.	2012	5	1	3	52°13'48.3"N 5°54'13.5"E
Achterpark E.	2012	5	1	3	52°14'20.7"N 5°54'25.5"E
Achterpark W.	2012	5	1	3	52°14'38.5"N 5°55'05.5"E
Dellen N.	2010	7	1	2	52°22'31.7"N 5°58'07.2"E
Dellen S.	2010	7	1	2	52°22'37.4"N 5°57'46.9"E
Ullerberg N.	2006	11	1	2	52°18'03.2"N 5°41'40.1"E
Garderen	2005	12	1	4	52°13'24.6"N 5°42'13.6"E
Epe N.	2004	13	1	2	52°23'04.9"N 5°57'27.3"E
Epe S.	2004	13	1	2	52°22'59.8"N 5°57'11.3"E
Ullerberg S.	1999	18	1	2	52°17'58.7"N 5°41'27.7"E
Gortel	1997	20	1	2	52°18'44.6"N 5°53'08.3"E
Hoenderloo	1984	33	2	3	52°09'22.9"N 5°52'53.1"E

A.2. Effect of ungulate fence and unfenced plots on 15 forest attributes related to structure (stem, sapling, pole, tree density, understory vegetation cover, Vaccinium, fern, shrub, moss, grass, other cover and canopy cover), composition (species richness, Shannon diversity, and conifer proportion) and litter depth. The mean and the 95% confidence interval of the mixed linear models are given.



A.3. Averaged tree species composition for fenced and unfenced plots in the 17 forest sites in the Veluwe, the Netherlands. Species composition is shown for a quadrat of 25 m².

	Establishment Year																
	2016	**2015**	**2014**	**2013**	**2012**	**2012**	**2012**	**2012**	**2010**	**2010**	**2006**	**2005**	**2004**	**2004**	**1999**	**1997**	**1984**
Species									**Fenced**								
Sorbus aucuparia	2,5	0,6	10,6	7,0	0,0	2,3	1,3	0,0	3,5	0,0	0,0	0,5	1,0	5,0	0,0	5,0	3,0
Amelanchier lamarckii	0,5	1,9	2,6	0,0	0,0	1,3	0,3	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,0	0,0	0,0
Betula pendula	5,5	2,5	7,3	36,0	26,3	0,3	0,0	2,0	25,5	61,0	55,0	40,5	5,5	49,0	6,0	7,0	3,7
Betula pubescens	0,0	0,0	0,2	6,0	0,0	0,0	0,3	0,0	0,0	0,0	0,0	1,5	0,0	22,0	0,0	1,0	0,0
Rhamnus frangula	0,5	0,1	4,5	18,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,0	7,7
Castanea sativa	0,0	0,0	0,0	0,0	1,3	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,7
Prunus serotina	0,0	0,0	0,2	0,0	0,3	0,3	0,0	0,0	1,5	17,0	0,0	0,0	4,0	0,0	0,0	0,0	0,0
Quercus robur	0,0	0,6	1,3	12,0	1,0	1,7	0,7	0,0	4,0	22,0	0,0	2,0	3,0	8,0	8,5	0,0	2,7
Quercus rubra	2,5	0,0	0,8	0,0	0,0	1,0	0,0	0,0	3,0	0,0	0,0	0,0	0,5	0,0	0,0	0,0	0,0
Populus tremula	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	35,0	0,0
Fagus sylvatica	0,0	0,1	0,0	0,0	0,7	0,0	0,7	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Larix kaempferi	3,0	0,0	0,2	0,0	0,0	0,0	0,0	0,0	47,0	4,0	0,0	0,3	1,0	0,0	0,5	0,0	0,0
Pinus sylvestris	20,0	9,2	18,8	29,0	2,3	0,7	2,3	2,0	30,5	49,0	135,0	28,8	2,0	51,0	23,0	0,0	0,7
Pseudotsuga menziesii	0,0	0,0	1,0	0,0	0,7	0,0	0,3	0,0	0,0	0,0	0,0	1,0	0,5	0,0	0,0	0,0	0,0
									Unfenced								
Sorbus aucuparia	6,5	0,7	3,5	5,5	0,0	0,7	0,3	0,7	0,0	0,0	0,0	3,3	0,0	0,0	0,0	0,0	0,2
Amelanchier lamarckii	0,0	1,5	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,3	0,0	0,0	0,0	0,0	0,0
Betula pendula	3,5	1,1	0,5	26,0	1,3	1,7	0,0	8,3	6,0	5,0	0,0	5,5	2,0	0,0	4,5	8,0	0,0
Betula pubescens	0,0	0,1	0,1	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Rhamnus frangula	3,5	0,2	2,9	10,5	0,0	0,0	1,0	0,0	0,0	0,0	0,0	1,5	0,0	0,0	0,0	0,0	0,5
Castanea sativa	0,0	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Prunus serotina	1,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Quercus robur	0,5	1,2	0,3	0,0	0,7	0,0	2,3	1,0	0,0	2,0	0,0	4,8	0,0	4,0	0,0	0,0	1,2
Quercus rubra	0,5	0,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Populus tremula	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Fagus sylvatica	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Larix kaempferi	0,5	0,0	0,2	0,5	0,0	0,0	0,0	0,0	29,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Pinus sylvestris	18,0	8,7	8,3	28,5	4,3	1,0	0,7	4,3	20,0	8,0	39,0	1,3	4,5	2,0	9,5	0,0	0,0
Pseudotsuga menziesii	0,0	0,0	0,5	0,0	0,3	0,0	0,0	0,0	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0