Direct and indirect effects of browsing on forest biodiversity

Evaluating the intermediate disturbance hypothesis in boreal forest ecosystems

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Abstract

Large mammalian herbivores (ungulates) are important drivers in forest ecosystems, but their effects on biodiversity and regeneration remain contested. This thesis examined the direct and indirect effects of ungulates on regeneration, vegetation structure, and biodiversity in Swedish boreal and boreonemoral production forests, with particular emphasis on the intermediate disturbance hypothesis (IDH). Using observational studies and ungulate-exclosure experiments, the thesis tested whether ungulate disturbance promoted biodiversity by reducing competition and increasing structural heterogeneity. Ungulate effects could not be explained by density alone. Moose density influenced browsing damage on Scots pine, but forest composition, competition, forage availability, and site productivity were also important. Browsing also constrained the development of palatable broadleaves. The biodiversity results provided partial support for the IDH. Vascular plant richness was highest at intermediate ungulate pressure, consistent with the idea that moderate disturbance can promote coexistence. This pattern was mediated largely through changes in vegetation structure, light availability, and habitat heterogeneity. Beetles also benefited from ungulate disturbance, but mainly through structurally open conditions and microclimatic change rather than a clear unimodal pattern. Overall, ungulates generated both ecological costs and benefits. The IDH helped explain some biodiversity responses, but not all, suggesting that co-management should move beyond density-based approaches and better account for vegetation structure, site conditions, and trade-offs between production and biodiversity.

Keywords: Ungulates, browsing, boreal forest, biodiversity, forest regeneration, intermediate disturbance hypothesis, vegetation structure, deer, moose, co-management

Direkta och indirekta effekter av betning på skogens biodiversitet. En utvärdering av den intermediära störningshypotesen i boreala skogsekosystem

Sammanfattning

Klövvilt är viktiga drivkrafter i skogsekosystem, men deras effekter på biologisk mångfald och föryngring är fortfarande omstridda. Denna avhandling undersökte klövviltets direkta och indirekta effekter på föryngring, vegetationsstruktur och biologisk mångfald i svenska boreala och boreonemorala produktionsskogar, med särskild betoning på hypotesen om intermediär störning (intermediate disturbance hypothesis, IDH). Med hjälp av observationsstudier och experiment med klövviltshägn prövades om störning från klövvilt främjade biologisk mångfald genom att minska konkurrens och öka strukturell heterogenitet. Effekterna kunde inte förklaras enbart av täthet. Älgtäthet påverkade betesskador på tall, men även skogssammansättning, konkurrens, fodertillgång och ståndortens produktivitet var viktiga. Betning begränsade också utvecklingen av begärliga lövträd. Resultaten gav delvis stöd för IDH. Kärlväxternas artrikedom var högst vid medelhögt betestryck, i linje med idén att måttlig störning kan främja samexistens. Mönstret förklarades främst av förändringar i vegetationsstruktur, ljustillgång och habitatheterogenitet. Även skalbaggar gynnades av betning, men främst genom öppnare struktur och förändrat mikroklimat snarare än genom ett unimodalt mönster. Sammantaget var betning förknippat med både ekologiska fördelar och nackdelar. IDH förklarade vissa men inte alla responser i den biologiska mångfalden, vilket tyder på att samförvaltning bör gå bortom täthetsbaserade angreppssätt och bättre beakta vegetationsstruktur, ståndortsförhållanden och avvägningar mellan produktion och biologisk mångfald.

Nyckelord: Klövvilt, betning, boreal skog, biologisk mångfald, skogsföryngring, intermediär störningshypotes, vegetationsstruktur, hjortdjur, älg, samförvaltning

Dedication

To my darling wife. I love you so very much.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Ó Cuív, C., Anderson, J., Berndt, C., & F. Widemo (2026). Predictors of browsing damage under co-management of boreal forests and deer. (manuscript)

II. Anderson, J., Hekkala, A.M., Ó Cuív, C., Berndt, C., Löf, M., & F. Widemo (2026). Impacts of browsing on regeneration and recruitment of palatable broadleaves in boreal forests. (submitted)

III. Anderson, J., Hekkala, A.M., & F. Widemo (2026). Intermediate browsing by diverse deer communities is linked to variation in vegetation structure and species richness in vascular plants. Forest Ecology and Management, 603 (2026), 123422. https://doi.org/10.1016/j.foreco.2025.123422

IV. Anderson, J., F. Widemo, Saggiomo, L., & Hekkala, A.M (2026). Browsing by deer generate variation in microclimates and influence biodiversity in ground-dwelling beetles. (manuscript)

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The contribution of Joseph Anderson to the papers included in this thesis was as follows:

I. Data curation, formal analysis, writing: review and editing

II. Investigation, data curation, formal analysis, visualisation, writing: original draft, review, and editing

III. Investigation, data curation, formal analysis, visualisation, writing: original draft, review, and editing

IV. Investigation, data curation, formal analysis, visualisation, writing: original draft, review, and editing

List of figures

Abbreviations

CV	Coefficient of variation
DER	Deer energetic requirement
GLMM	Generalised linear mixed modelling
HDDE	High deer density experiment
IDH	Intermediate disturbance hypothesis
LGE	Latitudinal gradient experiment
MMA	Moose management area
RAWO	Rowan, aspen, willow, oak
ÄBIN	Älgbetesinventering (Moose browsing inventory)

AI declaration

During the preparation of this work the author used ChatGPT (OpenAI) in order to receive support in troubleshooting and refining R code for data analysis. After using this tool/service, the author reviewed and edited the content as needed and take full responsibility for the content of the published work. These tools were not used in any other aspect of preparing this thesis.

“A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.”
— Aldo Leopold, *A Sand County Almanac*

1. Introduction

1.1 Ungulates as ecological engineers in boreal forests

Large mammalian herbivores (hereafter ungulates) are important drivers of ecosystem function in forested landscapes (Hobbs 1996; Pringle et al. 2023). Through browsing, grazing, trampling, nutrient deposition and other forms of disturbance, ungulates change plant community composition, alter competitive interactions, and modify the physical structure of the environment (Suominen & Danell 2006; Díaz et al. 2007; Foster et al. 2014). In boreal and boreonemoral forests, where light, competition, and stand age strongly regulate vegetation dynamics (Chertov et al. 2003; Anyomi et al. 2022; Lindenmayer et al. 2022), ungulate disturbance is an important top-down process, acting primarily through browsing and associated effects on habitat structure and nutrient dynamics (Suominen et al. 1999; Sitters & Andriuzzi 2019; Chevaux et al. 2022). The ecological effect of ungulates therefore extends beyond the direct removal of plant biomass and includes indirect effects mediated through changes to vegetation structure, microclimatic conditions, and habitat heterogeneity (Weisberg & Bugmann 2003; Ramirez et al. 2019).

These structural effects can occur across trophic levels (Ramirez et al. 2021). By changing the height, density, and cover of forest vegetation, ungulates alter the conditions under which plants compete and under which other organisms, such as insects, small mammals, and birds, use the habitat (Bernes et al. 2016; Afonso et al. 2024; Schwegmann et al. 2025). In this sense, ungulates may be understood as ecosystem engineers, whose impacts can shape regeneration trajectories, community composition, and biodiversity across spatial and temporal scales (Ramirez et al. 2018; Beguin et al. 2022).

The consequences of ungulate disturbances are also likely to depend on browser identity (Faison et al. 2016b; Hardalau et al. 2024). Larger cervids such as moose (*Alces alces*) differ from smaller deer species such as roe deer

(*Capreolus capreolus*) in obvious ways, such as body size and feeding height, but also in less obvious ways, such as diet and habitat use (Edenius et al. 2002; Schwegmann et al. 2023). These differences may lead to contrasting effects on forests and their associated biodiversity, depending on which ungulate species are present (Spitzer et al. 2021). Understanding the effects of ungulates in boreal and boreonemoral forests therefore requires attention not only to ungulate population density, but also to the community composition and the ecological context under which they occur.

1.2 Ungulate disturbances, regeneration and stand development

Browsing of young trees by ungulates has long been recognised as a key influence on tree regeneration in northern forest ecosystems (Beguin et al. 2016; Bernes et al. 2018). By removing shoots, suppressing growth, and altering competitive relationships amongst species, ungulates can affect both the abundance of regenerating trees and their probability of developing into healthy, tree-forming individuals (Ramirez et al. 2018; Kupferschmid et al. 2022). These effects are especially important in young forest stands, where vegetation development is rapid and competition for light and space is intense (Walters et al. 2020; Lettenmaier et al. 2025).

In Swedish production forests, these dynamics are particularly relevant for both commercially valuable conifers and ecologically valuable broadleaved tree species. Browsing on Scots pine (*Pinus sylvestris*) can reduce stem quality and suppress growth, leading to economic losses (Wallgren et al. 2014; Nilsson et al. 2016). As Scots pine is one of the most economically important tree species in Sweden (Mason & Alía 2000), browsing damage on pine has become one of the most visible points of conflict between forestry and ungulate management (Liberg et al. 2010; Dressel et al. 2021).

Other tree species are important because they help maintain biodiversity in boreal forests. Rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willows (*Salix* spp.) and oaks (*Quercus* spp.) support many associated species, including several of high conservation concern (Raspe et al. 2000; Berg et al. 2002; Enescu et al. 2016; Mölder et al. 2019). Their successful recruitment is therefore crucial for meeting biodiversity goals. However, they are also highly palatable and are often the preferred forage of ungulates during the summer months (Hörnberg 2001; Edenius et al. 2011; Myking et al. 2011). Ungulate disturbances can strongly affect their regeneration and alter the competitive dynamics in newly establishing stands, leaving these preferred species at a disadvantage.

These regeneration outcomes are not only determined by ungulate disturbances. Stand composition, density, and site productivity all shape how young forests develop (Pfeffer et al. 2021). Broadleaves may colonise quickly but still have limited chances of competitive success, and damage levels on commercially important species may depend more on forage availability than on ungulate densities (Dressel et al. 2021). In addition, silvicultural practices may have an equal or greater influence on regeneration, for example through selective pre-commercial thinning which often favours conifers over broadleaves (Fahlvik et al. 2015). Ungulate disturbances should therefore be understood as one component of a broader set of interacting processes that together determine regeneration and stand development.

1.3 Ungulates and biodiversity in forest ecosystems

Ungulate effects on biodiversity are complex, as their disturbances can both reduce and create ecological opportunities (Côté et al. 2004; Hegland et al. 2013; Bernes et al. 2018). By suppressing palatable plants through browsing and grazing, ungulates may limit some species and alter community composition. At the same time, ungulate disturbances can reduce structural dominance, increase access to light and space, and create more heterogeneous habitat conditions (Royo et al. 2010; Speed et al. 2014; Faison et al. 2016a). As a result, biodiversity responses to ungulate disturbance are often context dependent and may differ amongst taxa, spatial scales, and ungulate regimes (Bernes et al. 2018; Beguin et al. 2022; Schwegmann et al. 2025).

Figure 1. Spotted cat’s ear (*Hypochaeris maculata*), a species associated with grazing disturbance and other low-competition conditions. Although often found in meadow habitats, it can also occur in forest glades where grazing was once more intense, as shown here. Photo: J. Anderson

An important distinction is between direct and indirect effects. Ungulates may affect plant species directly through herbivory and physical disturbance, but many broader biodiversity responses are likely to arise indirectly through changes to forest structure (e.g. Speed et al. 2014; Daskin & Pringle 2016; Bernes et al. 2018). Variation in plant cover, community composition, stem density, vertical gap fraction (i.e. the proportion of open space in the vegetation when viewed vertically), and microclimatic conditions can all influence which plant species persist in the forest understory and, in turn, how animal communities are shaped through cascading trophic effects (Rainio & Niemelä 2003; Koivula 2011; Temperli et al. 2015; Sitters & Andriuzzi 2019). Taxa that respond strongly to habitat conditions, such as plants and relatively immobile ground-dwelling beetles, are likely to be particularly sensitive to ungulate induced changes in habitat structure (Suominen et al. 1999; Rainio & Niemelä 2003; Koivula 2011).

Broadleaved tree species provide an important example of the connection between ungulates and biodiversity. As noted above, rowan, aspen, willows and oaks support a diverse array of associated and specialised species, whilst also providing important ecological functions such as fruit production, pollen and nectar resources, and substrate availability (Raspe et al. 2000; Berg et al. 2002; Enescu et al. 2016; Mölder et al. 2019), particularly when individuals are allowed to develop into their mature trees (Tikkanen et al. 2006; Löf et al. 2016; Hardenbol et al. 2020). If browsing and interspecific competition prevent such species from recruiting successfully, the long-term biodiversity consequences may extend across trophic levels and far beyond the regeneration phase.

1.4 Ungulates and the intermediate disturbance hypothesis in boreal forests

The structural changes described above also connect ungulate ecology with broader disturbance theory. In some systems, species richness has been found to be maximised at intermediate levels of herbivory disturbance (e.g. Hegland et al. 2013; Gao & Carmel 2020), where herbivore action is sufficient to reduce competitive exclusion but not to the extent that sensitive or highly palatable species are lost (e.g. Royo et al. 2010; Fukamachi et al.

2023). This pattern is consistent with the intermediate disturbance hypothesis (IDH), which predicts that species richness is greatest in habitats where competition does not exclude less-dominant species, but mortality is not so high that only the most tolerant species persist (Connell 1978; Huston 2014; Schwegmann et al. 2025). Although such patterns are not universal (Fox 2013), they suggest that ungulate disturbance does not affect biodiversity in a simple linear fashion, nor is it always associated with either positive or negative outcomes. Instead, ungulates may act as important agents of disturbance and habitat heterogeneity in otherwise relatively stable or simplified forest systems (Gill & Beardall 2001; Bernes et al. 2018; Schwegmann et al. 2025).

Figure 2. 'Vallflicka med boskap' (Shepherdess with Cattle), painted by the Swedish artist Olof Arborelius in the late nineteenth century. The painting evokes a historical period when Swedish forests were more strongly shaped by seasonal livestock grazing, contributing to disturbance regimes that differed from those of modern production forests. Public domain image reproduced from Wikimedia Commons.

This is also relevant from a historical landscape perspective. Before modern intensive forestry, Swedish forests were shaped by more extensive land use, including seasonal grazing by livestock (Ericsson et al. 2000; Kardell 2016). Such ephemeral land use likely contributed to more open and varied forest conditions, with consequences for species composition and biodiversity (Cui et al. 2014). In the early twentieth century livestock numbers in forested landscapes were relatively high, at least seasonally, while wild ungulate populations remained relatively low. In the present day this situation has approximately reversed, with greater populations of wild ungulates and much fewer livestock (Ericsson et al. 2000; Kardell 2016). This shift raises the question of whether modern wild ungulate populations can replace some of the ecological roles once associated with livestock in maintaining heterogeneous habitats and biodiversity, or whether contemporary ungulate disturbances follow the IDH or operate under fundamentally different conditions in today's production forests.

1.5 Swedish forest and ungulate co-management

In Sweden, the ecological effects of ungulate disturbances such as browsing have major practical relevance as both forests and ungulate populations are actively co-managed (Widemo et al. 2019; Pfeffer et al. 2021). Production forestry and wildlife management both aim to deliver important ecosystem services, such as the production of high-quality timber, wild game, recreational opportunities, and biodiversity conservation (Boman et al. 2011; Pfeffer et al. 2021). However, these objectives do not always align. Browsing damage on Scots pine has become one of the clearest examples of this tension, and in response Sweden has developed an adaptive co-management system for wild game and forests that includes formal management structures, monitoring programmes, and target indicators (Bjärstig et al. 2014; Widemo et al. 2025).

This system includes browsing inventories such as ÄBIN (*Älgbetesinventering*; the Swedish moose browsing inventory) and management planning within Moose Management Areas (MMAs), as well as targets for both acceptable damage levels and the recruitment of biodiversity important broadleaved trees (Bjärstig et al. 2014; Widemo et al. 2019). These targets are intended to support balanced decision making, but they also imply assumptions about how ungulate activity affects forests (Widemo et al. 2025). In practice, management has often focused strongly on ungulate population densities, especially moose abundance, as a lever through which damage and regeneration outcomes can be controlled (Pfeffer et al. 2021; Widemo et al. 2025).

However, if browsing and disturbance effects depend strongly on forest structure, competition, site conditions, and ungulate identity, management systems based too narrowly on ungulate density may fail to capture the ecological mechanisms that determine outcomes. This is particularly important when production and biodiversity objectives are considered simultaneously, as Swedish forest policy since 1993 has formally placed production and environmental goals on an equal footing (Wester 2015). However, ungulate management regimes that minimise damage to commercially valuable trees may not be the same as those which promote broadleaf recruitment or support forest biodiversity.

Figure 3. Moose (*Alces alces*) often browse in young forest stands, as this camera trap image shows. Browsing on commercially important species can create conflict between forestry and wildlife management. Photo: J. Anderson

2. Objectives of this study

Against this background, the overall aim of this thesis was to investigate how wild ungulates influence forest regeneration, vegetation structure, and biodiversity in Swedish boreal forests, and to evaluate the implications of these effects for the co-management of wild ungulate populations and production forests in Sweden.

More specifically, the thesis examined how ungulates determine forest damage, broadleaf recruitment, and biodiversity across different ecological contexts, and looked to identify the mechanisms through which these effects arise.

These objectives were addressed through the following research questions and associated working hypotheses:

What factors determine browsing pressures and associated forest damage?

I hypothesised that factors such as pine density, between-tree competition, and site productivity would be as important as ungulate density in predicting damage on Scots pine. I further expected that management objectives based on target browsing thresholds would not be consistently achievable through moose population reduction alone.

How does browsing influence the recruitment and development of palatable broadleaved trees important for biodiversity?

I hypothesised that browsing would constrain the recruitment of broadleaved species, particularly their development into competitive height classes, but that browsing would not be the only limiting factor. I expected recruitment outcomes to also depend strongly on interspecific competition with conifers and site productivity.

How does browsing affect biodiversity in vascular plants and ground-dwelling beetles?

I hypothesised that browsing would influence biodiversity through changes in vegetation structure and habitat conditions, and that these effects would differ depending on the taxonomic groups. I expected vascular plant richness to be highest at intermediate browsing pressure, while for ground-dwelling beetles I expected browsing to promote local biodiversity by maintaining more open and structurally heterogeneous habitats.

Are browsing effects on regeneration and biodiversity mediated through changes in vegetation structure, competition, and microclimate?

I hypothesised that the main effects of browsing on biodiversity would be indirect and would work through changes in vegetation structure and microclimate, whereas effects on tree regeneration would reflect both direct browsing impact and the indirect effects of competitive interactions and site conditions.

3. Method

3.1 Study system

The studies included in this thesis were conducted in Swedish boreal and boreonemoral production forests. These forest landscapes are shaped by active silviculture and are inhabited by several large mammalian herbivores, primarily moose, roe deer, red deer (*Cervus elaphus*), and fallow deer (*Dama dama*). Wild boar (*Sus scrofa*) are also present, although their role as agents of forest damage is broader and less directly linked to browsing than that of wild cervids (Barrios-Garcia & Ballari 2012; Brunet et al. 2016; Matas et al. 2021). Across the thesis, particular emphasis was placed on young managed stands and production forest landscapes, where browsing interacts strongly with forest regeneration, vegetation development, and biodiversity (Pfeffer et al. 2021).

The Swedish forest landscape provides a useful system for studying browser impacts because it combines intensive forest management with comparably high and spatially variable ungulate densities (Spitzer et al. 2020, 2023; Pfeffer et al. 2021). It also includes a well-developed monitoring network for both forest condition and ungulate related browsing pressure (Bjärstig et al. 2014; Widemo et al. 2025). This made it possible to examine browsing effects across broad spatial gradients and under realistic management conditions. In turn, these effects can be directly linked to current challenges in the co-management of ungulates and forests.

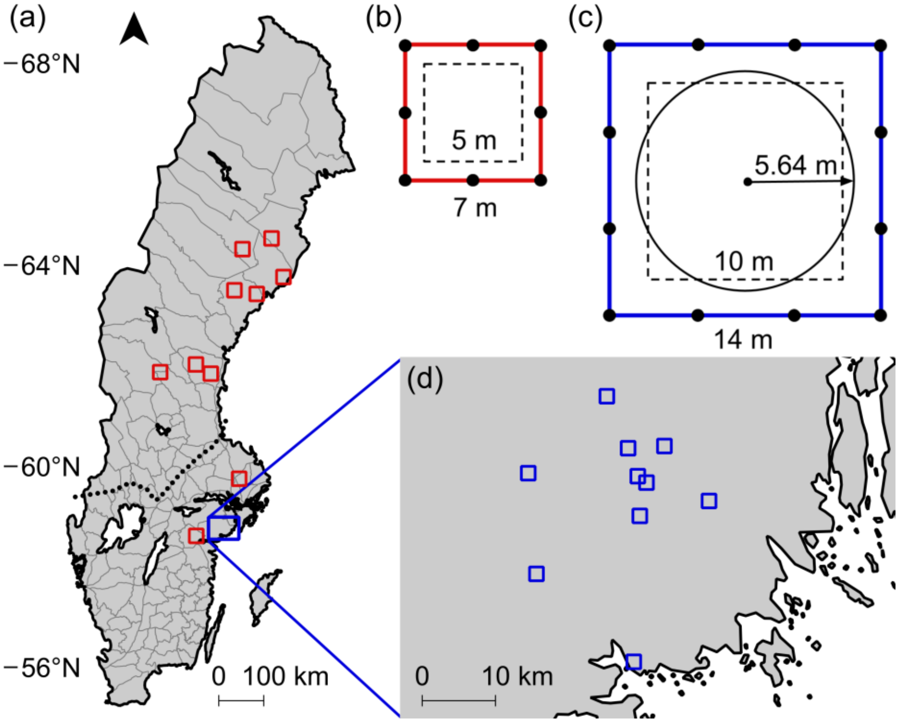

Figure 4. Locations of the stands with exclosures across a Latitudinal Gradient in Sweden (red boxes; LGE) and the position of the study area with High Deer Densities in the county of Södermanland (blue boxes; HDDE). Grey outlines indicate the location of the 129 moose management areas (MMAs) within Sweden. Observational data were collected both from the MMAs and from a plant species inventory conducted in tracts within the HDDE. The dotted line marks the approximate position of Limes Norrlandicus, a major biogeographical transition zone in Sweden separating hemi-boreal and boreal ecosystems; oak distribution occurs primarily south of this line (Sjörs 1999). (d) Enlarged map of the HDDE study area, showing the distribution of experimental stands (blue boxes). (b) Extent of the exclosures in the LGE (solid red), with all measurements conducted within the dashed inner buffer area (5 × 5 m). (c) Layout of the HDDE, indicating the full exclosure footprint (solid blue line), the 10 × 10 m measurement area (dashed square) where the tallest five rowan, aspen, willow and oak (RAWO) individuals were measured, and the circular plot (radius 5.64 m).

Figure 5. A typical young production forest stand just outside of Sveg in northern Sweden. In this stand the field-layer is dominated by lichens, showing the variation in plant communities across the Swedish forest landscape. An ungulate exclosure can be seen in the background. Photo: J. Anderson

3.2 Observational data sources

The observational components of the thesis drew on national and regional monitoring data, including forest inventories, browsing damage surveys, forest vegetation surveys, pellet-count estimates of ungulate density, and other environmental covariates. In Papers I and II, large-scale datasets from management were used to assess how browsing damage and broadleaf recruitment varied in relation to ungulate densities, forest composition, and site conditions. In Paper III, long-term pellet counts were used to estimate variation in deer density and community composition, which were then related to field-layer plant richness and vegetation structure which I had surveyed in the same tracts. Here we also derived an index for Deer Energetic Requirement (DER) by converting species densities to Kleiber-scaled metabolic demands and summing across species (Kleiber 1947). This allowed the total effect of the ungulate communities to be estimated on the same scale.

These observational datasets provided broad geographic coverage and high management relevance. They also allowed analysis across different forest conditions and, where relevant, across latitudinal gradients in climate, productivity, and vegetation characteristics. However, because observational patterns may reflect multiple interacting processes, they were interpreted together with the results from the experimental studies.

Figure 6. Field survey of forest floor vascular plants in a Swedish production forest. Observational vegetation surveys such as this were used in combination with pellet counts to assess relationships between ungulate density, vegetation community structure, and field-layer plant richness. Photo: S. Weréen

3.3 Experimental approaches

The experimental part of the thesis was based on ungulate-exclosure experiments in young forest stands. These exclosures were used to compare vegetation development and biodiversity in fenced plots, where ungulates were excluded, with unfenced control plots exposed to ambient browsing and other disturbances. In Paper II, exclosures were used to evaluate how ungulates affected the establishment and competitive development of rowan, aspen, willow and oak under different productivity conditions. In Paper IV, exclosures were used to assess how ungulate exclusion altered vegetation structure, microclimate, and beetle assemblages across a broad latitudinal gradient.

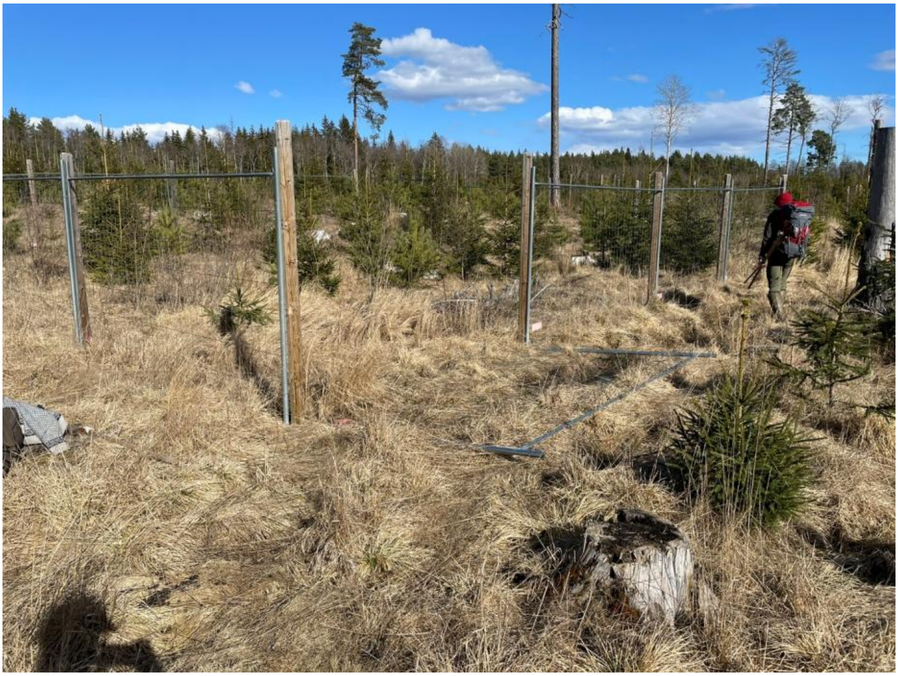

Figure 7. Measuring tree growth in a fenced ungulate exclosure in a young production forest stand. Experimental plots such as this were used to evaluate browsing effects while controlling for background variation in forest and landscape conditions. Photo: J. Anderson.

The experimental aspects of this thesis were particularly important for evaluating whether observed relationships could be attributed to the presence of ungulates themselves (and thereby, their behaviours, including browsing) rather than only to correlated variation in forest or landscape conditions. Importantly, they also made it possible to explore the mechanisms through which ungulates influence regeneration and biodiversity.

3.4 Combining observational and experimental methods

A major strength of this thesis lies in the combination of observational and experimental approaches. The observational studies provide broad-scale ecological ‘realism’ and are directly relevant to management challenges, while the experiments allowed stronger inference about causal mechanisms. Together, these approaches made it possible to assess both the general patterns and the underlying processes behind them.

The combined design was particularly important because the effects of ungulate disturbance are often context-dependent (Speed et al. 2014; Bernes et al. 2018; Beguin et al. 2022). Observational analyses revealed how browsing outcomes varied across landscapes, ungulate communities, and site conditions, whereas the exclosure studies clarified how ungulates influence vegetation structure, competitive interactions, microclimate, and biodiversity under controlled field conditions. By integrating these approaches, this thesis was able to address ungulate disturbance effects across multiple ecological response variables and spatial scales.

Figure 8. Field measurement of near-surface microclimatic conditions in a forest stand. Such measurements were used to assess how ungulate exclusion altered the local physical environment. Photo: J. Anderson

3.5 Statistical approaches

Most analyses in this thesis were based on generalised linear mixed modelling (GLMM), which was used to examine relationships between ungulates, regeneration, vegetation structure, and biodiversity across a range of response variables. In addition, Bayesian modelling was used in Paper I to predict management outcomes related to moose density and browsing damage on Scots pine, allowing for uncertainty in parameter estimates and predictions to be quantified more explicitly. For analysis of species diversity in Paper III, rarefaction approaches were also applied to increase the robustness of comparisons when sampling effort or the number of individuals differed between treatments. Together, these approaches made it possible to analyse a broad range of ecological responses using methods appropriate to the structure of the data and the aims of each study.

3.6 Overview of methods used in the included papers

- Paper I: large-scale observational analysis of browsing damage using browsing inventory data, ungulate density estimates, and environmental variables including weather data

- Paper II: combined observational and exclosure-based experimental study of the recruitment and development of rowan, aspen, willow and oak

- Paper III: observational analysis linking long term pellet-count estimates of deer density and community composition to vegetation structure and vascular plant richness

- Paper IV: large scale exclosure experiment examining the effect of ungulate exclusion on vegetation structure, microclimate, and ground-dwelling beetle communities

4. Results and discussion

4.1 Browsing effects cannot be understood through herbivore density alone

Browsing damage in boreal production forests is often framed as a problem of herbivore density, where high numbers of ungulates are assumed to lead directly to undesirable levels of forest damage, or even failed regeneration (Côté et al. 2004; Tremblay et al. 2004; Liberg et al. 2010; Fukamachi et al. 2023). This framing has strongly influenced management in Sweden, where reducing ungulate densities has been a central strategy for limiting forest damage and improving conditions for regeneration (Bjärstig et al. 2014; Widemo et al. 2019; Pfeffer et al. 2021). However, such a perspective risks oversimplifying the ecological processes that shape browsing outcomes. The results of this thesis suggest that while browser density is important, it does not determine whether targets for forest damage and regeneration are met.

Paper I showed that moose density was indeed an important predictor of browsing damage on Scots pine, confirming that ungulate abundance remains highly relevant for management. At the same time, pine stem density was equally, or more, important but as an opposite predictor, with higher densities of pine associated with lower browsing damage. This suggests that browsing damage is not only shaped by the number of ungulates present, but also by the availability and distribution of forage within the landscape. The finding that current damage target thresholds are difficult to achieve through ungulate density reduction strongly suggests that management cannot solely rely on ungulate population control to achieve these targets.

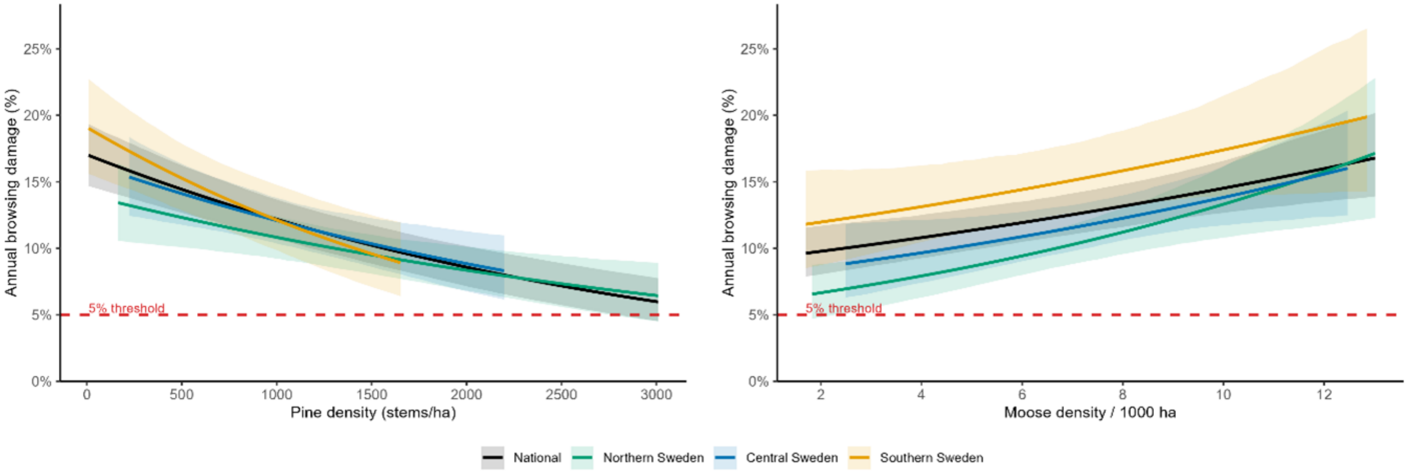

Figure 9. Predicted annual browsing damage (y-axis) as a function of the effect estimates for pine density (stems/ha) (left plot) and moose density / 1000 ha (right plot) derived from Bayesian beta regression models. The dashed red line marks the target threshold set by management for maximum 5% annual damage. Notably, the predicted damage levels remained above the target threshold, even at very high pine densities and very low moose densities, illustrating how difficult the current targets may be to achieve through changes to these parameters alone.

Paper II revealed a similar pattern, but from the perspective of broadleaf recruitment rather than browsing damage on pine. Browsing constrained the development of rowan, aspen, willow and oak, particularly by limiting their transition into competitive height classes. However, browsing was not the only factor determining recruitment outcomes. Site productivity and conifer density were often stronger predictors of whether recruitment targets were met than ungulate density itself. Experimental results further demonstrated that recruitment could remain below target levels even in the complete absence of browsing. This was especially the case on sites of intermediate productivity where some of these broadleaved species, especially oak and rowan, were outcompeted by faster growing conifers, whereas recruitment goals were met under very high ambient browsing pressures on rich soils. This suggests that broadleaf recruitment depends not only on browsing pressure, but also on the competitive dynamics of developing new stands and on local site conditions.

Together, Papers I and II show that browsing outcomes are shaped by the interaction between herbivore pressure and forest context, rather than just by browser density alone. While ungulate abundance clearly matters, the results demonstrate that browsing damage and regeneration success also depend on factors such as forage availability, stand composition, interspecific competition, and site productivity. Thus, management targets may remain difficult to achieve, even when ungulate populations are reduced. This suggests that management needs to account more explicitly for stand structure, competition, and site productivity, in order to create a more balanced and realistic approach to co-management.

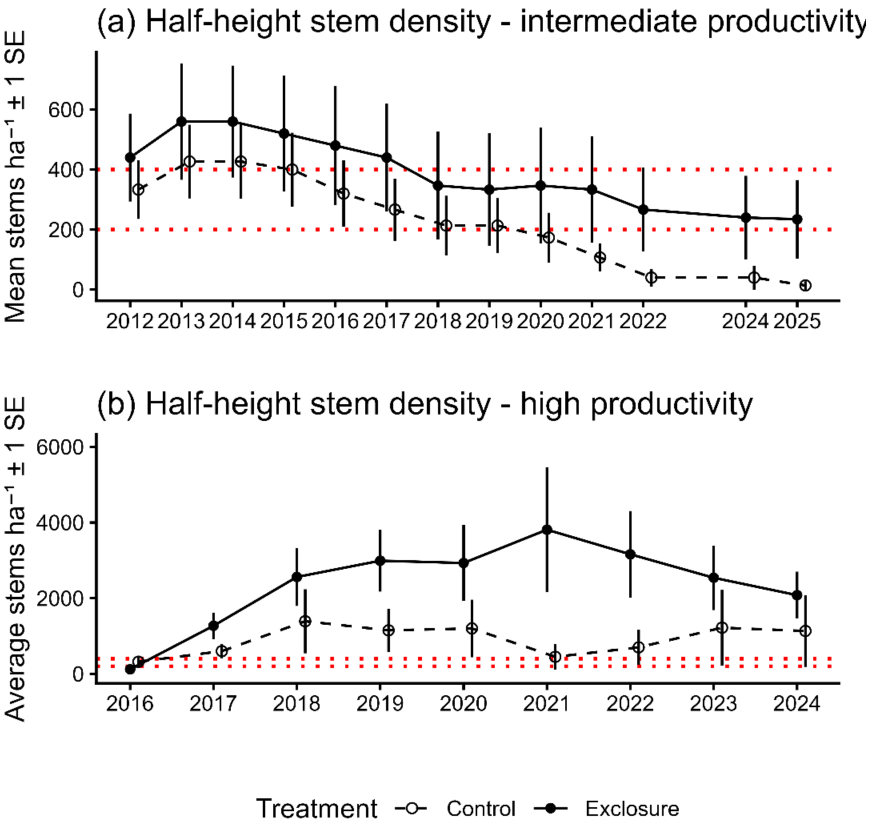

Figure 10. Density of rowan, aspen, willow, and oak (RAWO) stems per hectare exceeding half the height of the tallest production stems in the intermediate-productivity LGE (a) and high-productivity HDDE (b) experiments. Points and lines show treatment means ± 1 SE for exclosures and browsed controls. Red dotted lines indicate current Swedish recruitment targets. Browsing reduced the number of competitively developing RAWO stems, but stem densities also declined below target levels in exclosures at intermediate productivity, showing that browsing alone did not determine recruitment success.

4.2 Structural change as a shared mechanism of ungulate effects

One of the clearest patterns across this thesis was that ungulate disturbance effects were not only caused by the direct removal of biomass, but also by changes in forest vegetation structure (Suominen et al. 1999; Speed et al. 2014; Bernes et al. 2016). Across Papers II, III and IV, ungulates altered the height, density, cover, and composition of the plant community, and these changes influenced both regeneration and biodiversity. This makes vegetation structure the clearest shared mechanism linking the different responses examined in this thesis. In this way, ungulates altered the ecosystem, reshaping the structures through which ecological interactions and cascading effects occur (Bernes et al. 2018; Sitters & Andriuzzi 2019).

In Paper II, this mechanism was evident in the development of broadleaved tree species important for biodiversity. The presence of ungulates reduced the height growth of rowan, aspen, willow and oak, and limited their transition into competitive size classes, even though establishment had occurred successfully. Many stems were subsequently overtopped by faster growing conifers, although the strength of this pattern differed amongst species. Recruitment 'failure' was therefore linked not only to whether stems were present, but how stand development unfolded over time.

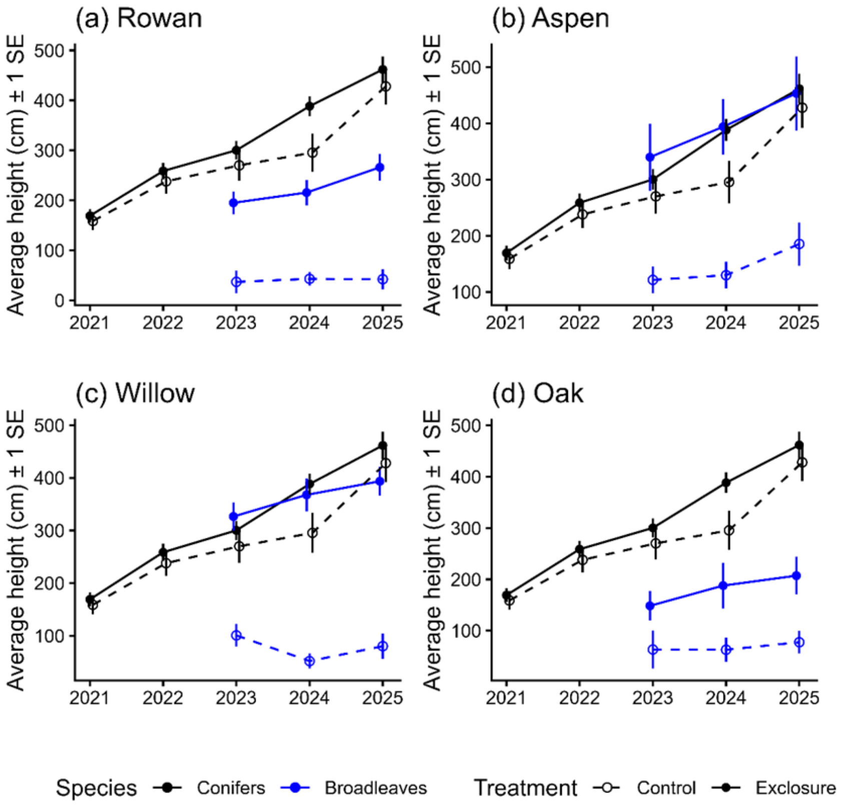

Figure 11. Average height (cm) of the tallest individuals of rowan (a), aspen (b), willow (c), and oak (d) compared to the average height of the two tallest conifers in exclosures and control plots in the experiment on soils of high productivity and high deer densities experiment (HDDE). Broadleaves are shown in blue and conifers in black. Points and lines are treatment means ± 1 SE (Fenced exclosures: solid symbols and lines; open controls: dashed lines and open symbols). The figure shows that all species remained shorter than conifers in browsed control plots, while in exclosures aspen and willow were able to keep pace more closely with conifers, whereas rowan and oak remained overtopped.

In Paper III, ungulate densities were linked to changes in field-layer structure, including variation in woody shrub cover, herbaceous species cover, and light availability through vertical gap fraction. These differences were associated with changes in field-layer plant species richness, indicating that ungulates influenced biodiversity through changes in vegetation composition and habitat openness. By reducing the dominance of some species, and by increasing the access to light and space for others, ungulates appear to modify the conditions under which forest field-layer plant communities develop. This implies that ungulate activity can function as an important driver of habitat heterogeneity and disturbance in otherwise relatively stable production forestry regimes.

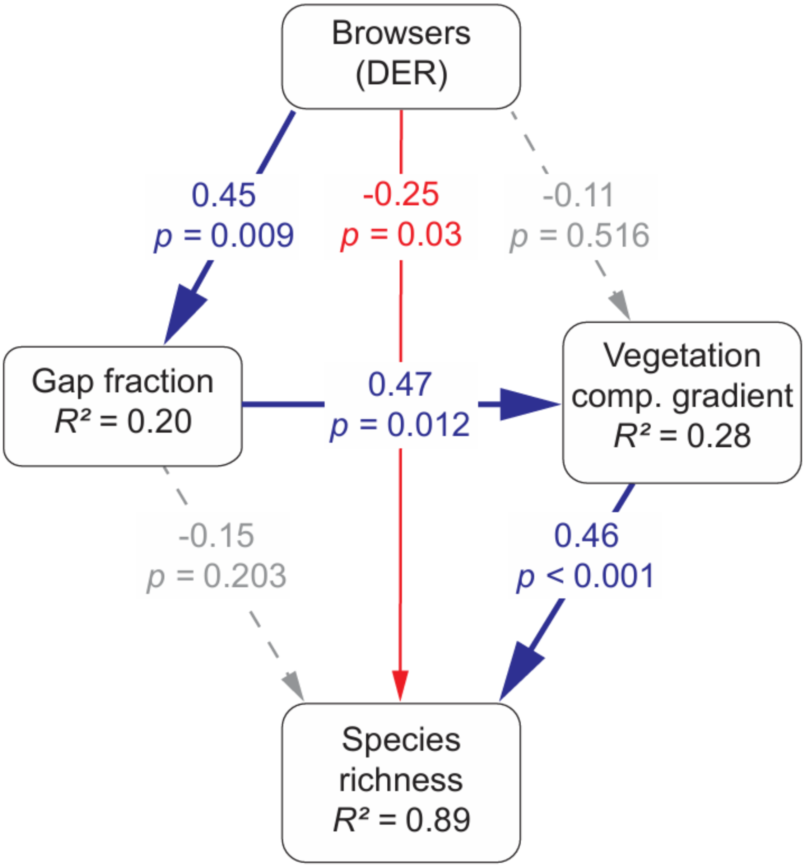

Figure 12. Structural equation model of deer energetic requirement (DER), vegetation composition gradient, and plant species richness. Solid arrows denote significant paths ($p < 0.05$), with blue arrows indicating positive relationships and red arrows indicating negative relationships. Dashed grey arrows denote non-significant paths. Numbers within arrows represent standardised estimates and significance level. R^2 values shown within boxes indicate the variance explained for each response variable; for species richness these represent Nagelkerke R^2 values. The model indicates that ungulate effects on species richness were primarily indirect, operating through changes in vegetation structure and composition rather than through a direct pathway alone.

Paper IV provided further experimental support for this mechanism. Ungulate exclusion increased tree stem density and field-layer plant cover, and also altered microclimate conditions, specifically diurnal temperature range. These changes were associated with lower beetle richness in exclosures, despite no clear differences in abundance. The results suggest that ungulate disturbance affected ground-dwelling beetles indirectly through changes to habitat structure and microclimate. As in Paper III, the biodiversity responses appeared to arise less from direct disturbance than from ungulate induced changes in the conditions experienced by other organisms. Interestingly, whilst local richness was higher in open control plots, species turnover was greater in exclosures. This suggests that ungulates also alter the heterogeneity and spatial organisation across plots, indicating that ungulate driven changes influence both local richness and variation in community composition across the landscape.

One possible explanation is that ungulate activity itself is patchy, such that the variation in site use creates a ‘browsing mosaic’, where vegetation structure and microclimate conditions vary strongly among plots. This interpretation is consistent with our own pellet count data (currently unpublished), where estimated ungulate density varied greatly both within plots over time and between plots over space (CV = 0.65). This suggests ungulate driven changes influence both local richness and variation in community composition across spatial and temporal scales.

Overall, Paper II, III and IV show that changes in vegetation structure formed the main shared mechanism through which ungulates influenced regeneration and biodiversity in this thesis. Browsing altered competitive dynamics amongst plants, the vertical structure and density of regenerating trees, the composition of the field layer, light dynamics, and local microclimatic conditions. These changes affected both plant and beetle communities, as well as the recruitment of important umbrella species. Ungulates therefore influenced the ecosystem not only by removing biomass directly, but also by reshaping the structural environment in which other ecological processes unfolded. This was one of the clearest patterns across the four papers.

4.3 Biodiversity responses to browsing are non-linear and taxon-dependent

Ungulates did not affect biodiversity in a uniformly positive or negative way across this thesis. Instead, responses differed amongst taxonomic groups and depended on both the community composition and abundance of ungulates present. One important pattern was that biodiversity responses could be non-linear, with intermediate browsing associated with higher diversity in some cases. Another was that different browser groups appeared to have different ecological effects, suggesting that ungulate identity matters as well as disturbance pressure itself.

In Paper III, vascular plant richness peaked at intermediate densities of small deer, supporting an intermediate disturbance pattern. Both low and high browsing levels were associated with lower richness, suggesting that moderate browsing created conditions that were more favourable for a diverse field-layer community. As discussed in the previous section (4.2), this relationship appeared to be mediated largely through changes in vegetation structure, including variation in dwarf shrub cover, graminoid cover, and vertical gap fraction. At intermediate browsing levels, ungulates likely increased species richness by reducing the dominance of strong competitors for light and space, such as dwarf shrubs, increasing vertical gap fraction through the removal of taller shrubs and saplings, and creating conditions that favoured the establishment of more species-rich groups such as graminoids and forbs. At higher browsing intensities, however, these positive effects may have been offset by increasing suppression or loss of more palatable species.

Paper III also showed that ungulate identity mattered, as moose, red deer, and small deer did not show the same relationship with vascular plant richness. Richness peaked at intermediate densities of small deer, whereas the relationship with moose density was negative, and no clear relationship was found for red deer. This suggests that different browser groups are not functionally interchangeable in their effects on field-layer diversity. A likely explanation is that ungulate species differ in body size, feeding behaviour, diet and habitat use, and therefore modify vegetation structure in different ways (Edenius et al. 2002; Spitzer et al. 2020; Schwegmann et al. 2023).

Biodiversity outcomes therefore depend not only on ungulate density, but also on ungulate community composition.

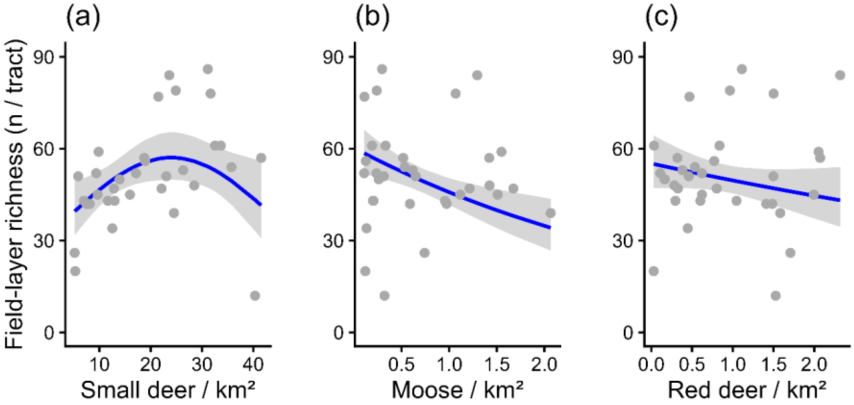

Figure 13. The relationship between browser species/group and total plant species richness of the field-layer. Panels show the relationship between field-layer richness and average density of small deer (a), moose (b), and red deer (c) as modelled by generalised linear models. Points represent the average values per tract, blue lines represent the modelled fit, and grey ribbons represent a 95 % confidence interval. The figure illustrates that species richness responded differently to ungulate identity, with richness peaking at intermediate densities of small deer, declining with increasing moose density, and showing no clear relationship with red deer density.

Paper IV showed a different but complementary biodiversity response, as beetle richness was lower in exclosures than in open control plots despite denser vegetation and the absence of ungulates. Reduced ungulate disturbance therefore did not increase local diversity. Instead, ungulate activity appeared to maintain habitat conditions that supported higher local beetle richness, even though exclosures showed greater turnover amongst plots; that is, beetle communities in exclosures were less similar to one another from plot to plot. This highlights that biodiversity responses depend not only on how much vegetation is present, but on how disturbances created by ungulates shape habitat structure and environmental variation. It also shows that responses differ amongst taxa and cannot be inferred from vegetation quantity alone.

Considered together, Papers III and IV show that biodiversity responses to ungulate disturbances depended on taxon, scale, and browsing regime. Low ungulate density was not automatically better for biodiversity, but neither was high density universally beneficial. Rather, ungulates created different outcomes for different taxonomic groups depending on how they altered vegetation structure and habitat conditions. These findings suggest that biodiversity cannot be managed through a single assumed optimum level of ungulate disturbance.

4.4 Management targets and ecological reality

Current co-management of ungulates and forests in Sweden relies heavily on thresholds and target indicators intended to reflect acceptable browsing damage and desired regeneration outcomes. Such indicators often imply that these outcomes can be controlled mainly through changes in ungulate population density. However, the results of this thesis suggest that this view is too simplistic. In several cases, current targets did not align closely with the ecological processes that actually determined damage levels or recruitment success.

Paper I showed that current thresholds for browsing damage on Scots pine are difficult to meet through ungulate population management alone. Although moose density was an important predictor of damage, pine stem density was also strongly related to browsing levels, showing that damage is a result of both herbivore pressure and forest conditions. Pine damage thresholds therefore reflect the interaction between ungulate population density, site conditions (particularly site productivity) and forage availability within the landscape.

Paper II pointed to a similar mismatch between management targets and ecological reality. Current RAWO targets reflect stem presence and early recruitment more so than long-term recruitment into competitive, tree-forming individuals. Although ungulates constrained broadleaf development, site productivity and conifer competition were also critical, and targets may be missed even in the total absence of ungulates. This suggests that the current management system may overattribute outcomes to ungulate browsing alone, and that they do not capture the ecological processes that determine successful broadleaf recruitment over time.

Notably, the primary objective for tree-forming individuals was still achieved, suggesting that recruitment dynamics extend over longer time frames than those we measured in the young-stand phase.

4.5 Trade-offs in the co-management of ungulates and forests

A central challenge in the co-management of ungulates and forests is that it involves balancing multiple objectives rather than solving a single, clearly defined problem. Ungulate disturbances can simultaneously generate negative outcomes for forest production and regeneration, while also contributing positively to structural heterogeneity and biodiversity. This means that different management goals may end up in conflict with each other in practice. The results of this thesis therefore point to trade-offs, rather than to one ecological optimum that would satisfy all objectives at the same time.

From a production and regeneration perspective, lower browsing pressures may often appear desirable. As shown in Papers I and II, ungulates can generate both economic and silvicultural costs, particularly through damage to timber quality in Scots pine and the constraints on the development of broadleaved tree species important for biodiversity. These findings show clearly that ungulate activity can work against both timber production objectives and the successful recruitment of ecologically valuable tree species. At the same time, ungulates can contribute positively to biodiversity by maintaining heterogeneity within forest stands. Paper III and IV show that ungulate disturbance is not automatically detrimental to biodiversity. Indeed, vascular plant richness and ground beetle diversity were both positively associated with ungulate presence, at least at intermediate levels. These findings suggest that the presence of ungulates in young forest stands can support and maintain biodiversity in several key forest taxa, even whilst generating costs for production and regeneration.

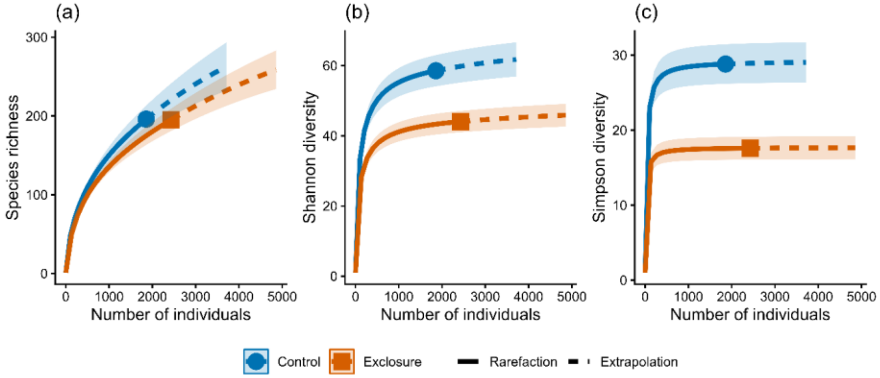

Figure 14. Rarefaction and extrapolation curves comparing ground-dwelling beetle assemblages in browsed control plots and fenced exclosures. Panels show (a) species richness (Hill number q = 0), (b) exponential Shannon diversity (q = 1), and (c) inverse Simpson diversity (q = 2) as functions of the number of individuals. Solid lines represent rarefaction and dashed lines represent extrapolation; shaded areas indicate 95% confidence intervals. Beetle diversity was consistently higher in browsed control plots, particularly for Hill numbers 1 and 2, indicating that ungulate presence favoured the diversity of common and dominant species.

Taken as a whole, these results suggest that some management objectives are inherently conflicting. The ungulate management regime that minimises pine damage is unlikely to maximise forest biodiversity at the same time. No single ungulate density or browsing regime can therefore be expected to optimise all outcomes simultaneously. Effective co-management must instead be based upon explicit priorities, local ecological context, and a clear recognition that trade-offs are unavoidable.

4.6 Strengths and limitations

An important strength of this thesis is the combination of large-scale observational analyses with experimental field studies. The observational studies made it possible to evaluate ungulate effects under realistic management conditions and across broad spatial gradients in Sweden, while the experiments allowed stronger inference about causal mechanisms. Together, these approaches provide a more robust understanding of how ungulates influence regeneration, forest structure and biodiversity than either approach would have done on its own.

However, several limitations should be acknowledged. Ungulate guilds differ in behaviour, diet, body size, and habitat use, and are therefore not fully interchangeable in their ecological effects (Edenius et al. 2002; Spitzer et al. 2020; Schwegmann et al. 2023). In addition, some of the inferred mechanisms in this thesis, particularly those linking ungulate activity to biodiversity through structural change, were not always measured directly but were instead inferred from observed associations amongst vegetation, light availability, local microclimate, and species response. These interpretations were well supported by the combined results, but they nevertheless remain simplifications of complex ecological systems.

Interpretation of the results is also limited by the temporal scale of the studies and by the types of biodiversity metrics used. Stand development, and in particular broadleaf recruitment, unfold over long periods of time. Some effects of ungulate disturbance may only become fully apparent in later stages of succession (Tremblay et al. 2004; Mathisen et al. 2010; Kolstad et al. 2018). Similarly, species richness represents only one aspect of biodiversity and does not capture all aspects of community composition, function, or conservation value. Though several other aspects of biodiversity were analysed during the course of this thesis, the patterns identified should be understood as important parts of the broader ecological picture, rather than as an exhaustive description of the effects of ungulate disturbances on Swedish forest ecosystems. Despite these limitations, the consistency of several patterns across studies and response variables strengthens the overall conclusions of this thesis.

5. Conclusions, management implications, and future perspectives

This thesis shows that large mammalian herbivores are important drivers of both regeneration and biodiversity in Swedish boreal and boreonemoral forests. Their effects were not limited to the direct removal of biomass, but were often mediated through changes in vegetation structure, competitive interactions, light conditions, and local microclimate. Across the included studies, ungulates influenced the development of key tree species, the composition and richness of field-layer plant communities, and the diversity of ground-dwelling beetles. Taken together, these results show that disturbances generated by ungulate activity cannot be understood from population densities alone but must instead be interpreted in relation to the environmental context in which they occur and the structural changes they create.

The findings also have clear implications for management. The results of this thesis suggest that ungulate population reduction alone is insufficient as a general management tool. For instance, pine damage depended on both browser numbers and forest composition, while broadleaf recruitment depended on browsing, competition, and site productivity. Additionally, the biodiversity results showed that lower ungulate densities are not necessarily the most desirable outcome, as several components of forest biodiversity benefited from intermediate levels of ungulate disturbance, or from the structural conditions maintained by their presence. Management should therefore move away from population control towards more ecologically realistic, objective-specific, and taxon-specific indicators that better reflect the biological processes underlying both production and biodiversity outcomes.

Several questions remain for future research and management. Longer time series and studies covering the later stages of stand development are needed to better understand the long-term consequences of ungulate activity on broadleaf recruitment and forest structure. There is also a need to include a wider range of taxa and biodiversity metrics, including functional and compositional measures, in order to capture the impacts of ungulate activity more fully. In addition, the contrasting responses associated with different ungulate groups highlight the importance of improving our understanding of ungulate identity and guild composition, rather than treating all ungulate browsers as functionally equivalent. Continued progress and a deeper understanding will therefore depend on integrating forestry and biodiversity perspectives more closely in both research and co-management.

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Popular science summary

Moose and deer do more than browse young trees in Swedish forests. By feeding on some plants and leaving others behind, they help shape which species can grow, how dense forests become, and what kinds of habitats are available for other organisms. This matters not only for forestry, but also for biodiversity.

This thesis explores how moose and deer influence both forest regeneration and biodiversity in Swedish production forests. The results show that their effects cannot be understood from animal numbers alone. What happens also depends on forest conditions, such as site productivity, forage availability, and competition between trees and other vegetation.

Moose and deer affect forests in both direct and indirect ways. Directly, they browse young trees, which can damage pine and restrict the growth of palatable broadleaved species. Indirectly, this browsing changes forest structure by making vegetation less dense and creating more variation in light, space, and habitat conditions. These structural changes can have important consequences for biodiversity.

We found that moderate ungulate disturbance increased plant diversity by reducing competition and allowing more species to coexist. More open and varied conditions also benefitted insects, including beetles, by creating warmer and more heterogeneous habitats. At the same time, strong browsing pressure reduced regeneration and made it harder for some tree species to develop.

Overall, the thesis shows that moose and deer create both ecological costs and ecological benefits in forest landscapes. They can reduce tree growth and cause damage that matters for timber production, while also helping to create forest conditions that support biodiversity. The results suggest that forest management should move beyond focusing only on ungulate numbers and instead balance production, regeneration, and biodiversity to build healthier and more resilient forests in the future.

Populärvetenskaplig sammanfattning

Älgar och hjortdjur gör mer än att beta på unga träd i svenska skogar. Genom att äta vissa växter men lämna andra påverkar de vilka arter som får fäste, hur tät skogen blir och vilka livsmiljöer som skapas för andra organismer. Det här är viktigt inte bara för skogsbruket, utan också för den biologiska mångfalden.

Denna avhandling undersöker hur älgar och hjortdjur påverkar både skogsföryngring och biologisk mångfald i svenska produktionsskogar. Resultaten visar att deras effekter inte kan förklaras enbart av antalet djur. Minst lika viktigt är hur skogen ser ut och vilka förutsättningar som råder på platsen, till exempel markens produktivitet, tillgången på foder och konkurrensen mellan träd och annan växtlighet.

Älgar och hjortdjur påverkar skogen både direkt och indirekt. Direkt genom att beta på unga träd, vilket kan skada tall och hämma tillväxten av viktiga lövträd. Indirekt genom att förändra skogens struktur: när växtligheten blir glesare ökar variationen i ljus, utrymme och livsmiljöer. Sådana förändringar kan få stor betydelse för den biologiska mångfalden.

Vi upptäckte att ett måttligt betestryck ledde till högre växtdiversitet, eftersom konkurrensen mellan växter minskade och fler arter kunde leva sida vid sida. Mer öppna och varierade skogsmiljöer gynnade även insekter, bland annat skalbaggar, genom att skapa varmare och mer heterogena förhållanden. Samtidigt försämrade ett högt betestryck föryngringen och gjorde det svårare för vissa trädarter att etablera sig och växa.

Sammantaget visar avhandlingen att älgar och hjortdjur ger upphov till både kostnader och nyttor i skogslandskapet. De kan skada unga träd och minska produktionen, men också skapa förhållanden som gynnar biologisk mångfald. Istället för att fokusera på antalet betesdjur behöver skogsbruket därför balansera produktion, föryngring och biologisk mångfald för att skapa förutsättningar för friskare och mer motståndskraftiga skogar i framtiden.

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III

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Intermediate browsing by diverse deer communities is linked to variation in vegetation structure and species richness in vascular plants

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A B S T R A C T

Natural disturbances, including herbivory by deer, are key drivers of forest dynamics, yet their role in shaping field-layer plant diversity remains unresolved. We investigated how variation in deer density and community composition relates to field-layer plant richness in boreonemoral forest, with reference to the Intermediate Disturbance Hypothesis (IDH). Using annual pellet counts from 2012 to 2023, we quantified long-term densities of moose (*Alces alces*), red deer (*Cervus elaphus*), and small deer (roe *Capreolus capreolus* and fallow *Dama dama* combined) across 33 1 × 1 km forest tracts in central Sweden. We derived a Deer Energetic Requirement (DER) index by converting species densities to Klieber-scaled metabolic demands and summing across species. In 2023, field-layer vascular plants were surveyed, and relationships between deer densities, vegetation structure, and species richness were analysed. Bilberry browsing increased with both small deer density and DER, confirming that density estimates reflect realised browsing pressure. Vascular plant richness showed a unimodal relationship with small deer density, consistent with the IDH. Contrastingly, field-layer richness had a negative relationship with moose population density, while no relationship was found for red deer. Intermediate levels of DER were associated with lower dwarf shrub cover and higher vertical gap fraction and graminoid cover. These structural differences appeared to be the main indirect pathway through which deer density was related to diversity. Our findings emphasise the importance of browser community composition, density, and heterogeneity in structuring boreonemoral field-layers. Moderate browsing, especially by small deer, can enhance plant diversity by mediating resource availability in forest ecosystems.

1. Introduction

Natural disturbances are central drivers of forest dynamics, shaping succession, maintaining biodiversity, and influencing nutrient cycling and forest structure (Bergeron et al., 2001; Rowe and Scotter, 1973). These disturbances are fundamental for maintaining forest resilience and ecosystem functioning (Angelstam and Kuuluvainen, 2004; White and Pickett, 1985). Disturbances created by wild cervid browsers and grazers (hereafter deer) are notably influential, shaping the forest field-layer (the low growing plants of the forest floor) through herbivory (Díaz et al., 2007), trampling, thrashing, and rooting (Foster et al., 2014; Suominen and Danell, 2006, p. 2). Deer also influence the spatial and temporal dynamics of nutrient inputs to forest soils through urination and defecation, thereby indirectly affecting biodiversity (Sitters and Andriuzzi, 2019). In combination, the effects of deer are thought to be a crucial determinant of plant community composition and dynamics in forests (Pastor et al., 1988; Suzuki et al., 2013). In the context of growing interest in nature-based solutions to biodiversity loss, understanding how large herbivores influence forest ecosystems has taken on renewed importance. Thus, the nature of the relationships between deer and biodiversity are of great interest to conservationists, forestry professionals, wildlife managers, and researchers alike.

Previously, studies have shown negative associations between deer density and the diversity of the field-layer, often reporting shifts from diverse communities of palatable woody species to more homogeneous communities composed of sedges, ferns, and grasses as the density of deer increases (e.g. Rooney, 2009; Frerker et al., 2014; Habeck and Schultz, 2015; Fukamachi et al., 2023). This has led researchers and managers to discuss deer densities in terms of 'overabundance' and to advocate for a reduction in deer densities in order to favour biodiversity (Côté et al., 2004). However, many other studies have shown positive impacts on plant diversity from increased browsing and grazing pressure, both in observational (Chevaux et al., 2022; Hegland et al., 2013; Royo et al., 2010) and experimental studies (Côté et al., 2014; Faison

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et al., 2016a; Reed et al., 2022), or have asserted that the responsiveness of plant communities is not easy to predict (Beguin et al., 2022; Faison et al., 2016b; Speed et al., 2014).

Hegland et al. (2013) showed that field-layer plant richness increased with red deer herbivory, but only up to natural levels. Thereafter, at artificially high browsing intensities (using enclosures), the diversity of plants decreased. These findings are consistent with the classical grazing-species richness curve, which suggests a maximum level of plant species richness at intermediate levels of grazing disturbance (Gao and Carmel, 2020). In boreal forests, such non-linear responses to browsing are plausible: moderate browsing can suppress competitive woody species, increase light and microsite availability and allow less competitive herbs and grasses to establish (Faison et al., 2016a, 2016b; Hegland et al., 2013; Royo et al., 2010; Trepel et al., 2025). Thereafter, very high browsing levels reduce overall field layer biomass and remove both dominant and sensitive species (Fukamachi et al., 2023; Habeck and Schultz, 2015; Rooney, 2009). These opposing processes create the conditions under which a hump-shaped richness pattern may arise across browsing gradients. This pattern follows the intermediate disturbance hypothesis (hereafter IDH), which states that moderate disturbance maximises biodiversity by preventing dominance of competitive species while avoiding the excessive mortality caused by high disturbance (Connell, 1978). While the IDH has been influential for understanding effects of grazing on biodiversity in open landscapes, its general applicability in boreal forests remains uncertain and understudied (Gill and Beardall, 2001; Schwegmann et al., 2025). Furthermore, the broader validity of the IDH has been questioned, with some authors claiming the empirical support is weak, the definitions are vague, and that alternative mechanisms may better explain the patterns seen (e.g. Fox, 2013; Huston, 2014; Mackey and Currie, 2001).

Evaluating the effects of browsing and grazing is complex, partly as deer differ greatly in body size, diet and behaviour (e.g. Hofmann, 1989; Spitzer et al., 2020). Thus, it is necessary to have accurate information about the composition of the deer community to predict the effects of browsing and grazing on biodiversity. Furthermore, the extent of disturbance will depend on a combination of the energy requirement of the deer community and the availability of forage, where increasing forage availability will result in a reduced browsing pressure for a given deer density and community composition (Bergman et al., 2001; Bergqvist et al., 2018; Frerker et al., 2013). To account for these differences in body size and energy needs, we introduce a standardised index of deer energetic requirement (DER), allowing the combined energy needs the deer community to be considered.

There have been relatively few studies testing the predictions from the IDH in boreonemoral forests and even fewer which have investigated the long-term effects of herbivory (Bernes et al., 2018). Here, we make use of long-term data to explore the relationships between deer population densities and the species richness of vascular plants across gradients in deer communities in a Swedish boreonemoral forest landscape. To verify that our density estimates reflected realised browsing pressure, we also scored bilberry shoot removal as an independent field indicator of browsing intensity.

We tested four specific hypotheses:

H1. – Intermediate browsing promotes peak richness: Field layer plant species richness shows a hump-shaped relationship to deer-browsing, with richness highest at intermediate deer density and lower at both low and high browser density.

H2. – Deer modify vegetation structure in predictable ways: Higher deer densities are associated with increased understorey light availability (higher vertical gap fraction) and reduce dwarf-shrub dominance.

H3. – Associations with richness are primarily indirect: In structural equation modelling, we would predict that species richness is more closely associated with variation in vertical gap fraction and vegetation structure as compared to DER.

H4. – Species-specific browsing effects: The magnitude and form of browsing effects differ between deer species (moose, red deer and small deer) as their body size and realised diets produce different browsing pressures and effects.

These dynamics are not only ecologically important but also highly relevant for management, since browsing pressure can limit commercial forestry yields (Reimoser et al. 1999; Apollonio et al. 2010; Hardalau et al., 2024), adding another layer of complexity to balancing objectives. By clarifying how deer communities shape plant diversity and forest structure, our results will support the co-management of forests and deer, where trade-offs must be found between game management, forestry, and conservation.

2. Material and methods

2.1. Study area

The study was conducted in central Sweden near Öster Malma, which lies in the boreonemoral transition zone (58.9° N, 17.1° E) (Fig. 1). This area is characterised by its mosaic landscape of boreonemoral forests, mires, and mixed agriculture. Common tree species include Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birches (*Betula pendula, B. pubescens*), aspen (*Populus tremula*), pedunculate oak (*Quercus robur*), black alder (*Alnus glutinosa*) and willows (*Salix* spp.). Within forest stands, the field layer is dominated by ericaceous dwarf shrubs (particularly of the genera *Vaccinium*, *Calluna*, and *Empetrum*), mosses and lichens. Although forests dominate in the landscape, about 20 % of the area is agricultural land consisting of small to medium-scale pastoral and arable farms. Common crops include leys (arable land used for hay, silage or grazing), cereals, and root vegetables.

Forests in the study area are managed under modern Scandinavian rotation forestry. A typical rotation begins with clear-cutting, followed by planting, pre-commercial thinning, and later commercial thinning, with the full rotation lasting ~65–90 years for conifers. Stands themselves form even-aged mosaic spanning all developmental stages at the landscape scale. The Swedish Forest Agency classifies stands ages according to management requirements, these being regeneration after clear cuts, young/pre-commercial thinning stands, intermediate aged thinning stands, mature stands ready for final felling, and low productivity / sparse forest unsuitable for forestry (Roberge et al., 2020).

The deer community present in the area is comprised of moose (*Alces alces*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and roe deer (*Capreolus capreolus*), which occur in sympatry. In this region, winter and summer ranges of deer overlap extensively (Spitzer et al., 2021). Wild boar (*Sus scrofa*) are also present throughout the landscape but their primary foraging impact is via rooting rather than foliar browsing and grazing (Bruinderink and Hazebroek, 1996; Brunet et al., 2016). Thus, we focus only on deer as browsers and grazers below. All four deer species are actively hunted in the region (Table 1), which contributes to annual population turnover. Wolves are now present at low densities within and around the study area, however, predation pressure is currently low and unevenly distributed and is not considered a major driver population dynamics (Svensson et al., 2025, 2022).

2.2. Sampling design

Our study of species richness was conducted in previously established 1 × 1 km (perimeter 4 km) tracts distributed systematically across the landscape (Fig. 1b) (e.g. Spitzer et al. 2021). Each selected tract contained 16 evenly spaced sampling plots along the 1 × 1 km perimeter, spaced 200 m apart and with no plots located in the corners (Fig. 1c). At each plot, both deer faecal pellet counts and vegetation surveys were conducted (Fig. 1d). We also recorded the logging class of the stand in which the plot was located, following the Swedish Forest

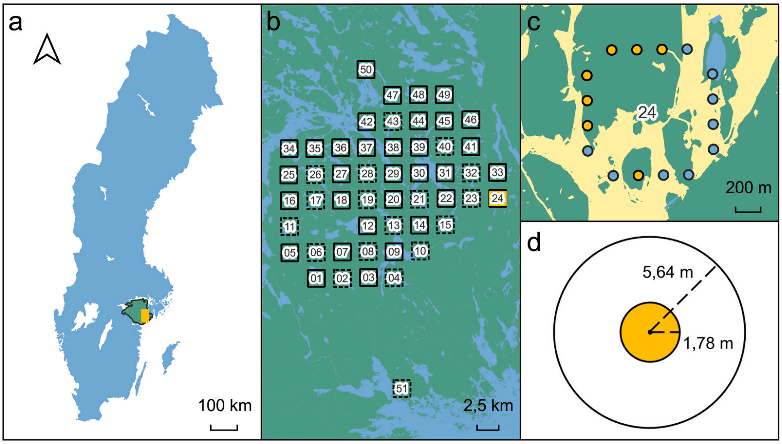

Fig. 1. The study area is located in southern Sweden (a) at the boreonemoral transition zone, the county of Södermanland is outlined and shown in green. The sampling was conducted using 1 × 1 km (perimeter 4 km) tracts (b), where sampling plots were systematically placed 200 m apart along the edge (c). Deer pellets were identified and counted in an area of 100 m^2 (radius = 5.64 m) or 10 m^2 (radius = 1.78 m) depending on the species. Vegetation identification and coverage surveys were recorded in an area of 10 m^2 (radius = 1.78 m) (d). Vegetation surveys were only conducted where a sampling plot occurred in forests and forest edges (yellow circles), whereas deer pellets were counted in all accessible plots (blue circles).

Table 1
Deer species densities (mean ± SE) near Öster Malma based on hunt harvest records and pellet count estimates (2012 – 2023).

Species	Harvest (individuals shot km^{-2})	Pellet counts (estimated individuals km^{-2})
Moose	0.14 ± 0.03	0.60 ± 0.03
Red deer	0.22 ± 0.12	0.80 ± 0.10
Fallow deer	6.32 ± 0.42	–
Roe deer	0.65 ± 0.02	–
Small deer *	–	18.90 ± 1.10

* Small deer = fallow deer + roe deer (pellet counts only).

Agency categories described above. Pellet count surveys were conducted every spring from 2012 onwards, whereas the vegetation survey was conducted during the summer of 2023. Due to time constraints, 33 out of 51 existing tracts were randomly chosen and monitored for species richness of vascular plants. Because field-layer vegetation in boreonemoral forests tends to change slowly and exhibit low turnover (Frerker et al., 2014; Hart and Chen, 2006; Suominen and Olofsson, 2000), the 2023 vegetation survey is expected to reflect vegetation states shaped over multiple years, consistent with our use of long-term (12-year) deer density estimates.

2.3. Estimated deer density

Though moose and roe deer differ greatly in size (up to 850 kg for an adult bull moose vs. ~35 kg for a roebuck), both considered concentrate selectors (species specialised on nutrient-rich, low-fibre forage such as forbs, buds and young leaves) *sensu* Hofmann (1989). In contrast, fallow deer and red deer are intermediate feeders that mix browsing and grazing. Previous studies from the same area have shown that the deer community composition shapes competition over forage and the resulting diets of the different species (Spitzer et al., 2021). We used pellet counts to determine the density of these deer populations and the composition of the deer community. We chose pellet-group counts as they are a standard monitoring tool in Fennoscandia (Månsson et al., 2011a, 2011b; Pfeffer et al., 2018) and elsewhere (Forsyth et al., 2007), and they correlate well with independent density estimates from aerial surveys, GPS collars, and camera trap estimates for moose and deer (Månsson et al., 2011a, 2011b; Pfeffer et al., 2018). Pellet counts have also been successfully used to elucidate ecological processes related to forage utilisation and competition within the deer guild in the same area previously (Spitzer et al., 2021).

Pellet count surveys were conducted each spring immediately following snowmelt in plots both on forested land and on agricultural land not subject to tillage (Fig. 1c), as such they represent deer densities in winter, when most browsing on dwarf shrubs and young trees occurs (Bergqvist et al., 2018; Cederlund et al., 1980; Spitzer et al., 2021). For moose and red deer, pellet groups were recorded within 100 m^2 plots (radius = 5.64 m, Fig. 1d), while the more abundant roe and fallow deer were surveyed within smaller, concentric 10 m^2 plots (radius = 1.78 m) centred at the same point. Only pellet groups deposited on top of last autumn's leaf litter were used for calculating annual winter densities. Estimates were corrected for the number of days between average date of leaf fall and monitoring (Bergström et al., 2019). Deer densities per 1 km^2 were estimated using the formula adapted from Bergström (2019):

$$\text{Density (individuals per unit area)} = S\,/\,(k \times P \times D \times T)$$

where:
S = total number of pellet groups counted for the species/group within sampled plots,
k = scaling constant depending on plot size and desired density unit,
P = number of plots surveyed,
D = average daily defecation rate (pellet groups per day) specific to each deer species or group,
T = number of days over which pellets accumulated.

Comparisons of data and densities from pellet counts between species requires knowledge of how many pellet groups an average individual produces per day. We used the following daily defecation rates: 16.5 for moose (Bergström et al., 2019), 19.0 for red deer (Dobiáš et al., 1996) 22.0 for fallow deer (Stubbe and Goretzki, 1991) and 22.0 for roe deer (Cederlund and Liberg, 1995). We used averages for 12 consecutive years of surveys to reduce annual stochastic variation in deposition or decay and provide a long-term deer density index.

Previous work in the same study area has shown that it is not possible to reliably distinguish between roe deer and fallow deer droppings without conducting DNA analysis (Spitzer et al., 2019). Therefore, roe deer and fallow deer were combined into the category "small deer" in pellet count surveys. This category completely dominated the deer community (Table 1.). In order to elucidate the composition of the ‘small deer’ category, we display harvest data from the same area for fallow and for roe deer for contrast (Table 1; Swedish Association for Hunting and Wildlife Management (SAHWM), 2025)

2.4. *Energy requirement of the deer community*

Furthermore, to enable rough comparisons of the relative energy demands of the deer community we calculated a combined ’Deer Energetic Requirement’ index (hereafter DER). DER expresses the relative daily metabolic energy demand per tract (as this is the spatial scale at which we compare the deer species) and is based on Kleiber’s law (Kleiber, 1947), which states an animal’s relative energy requirement is proportional to its body mass raised to the power of 0.75. Using average adult body masses from Wiklund and Malmfors (2014), one moose has the energetic requirement approximately equal to: two red deer, four fallow deer, or seven roe deer. Thus, DER allows all deer species to be placed on a common energy-demand scale, while acknowledging that their diets differ (Spitzer et al., 2023). For each tract and year, we multiplied the population density (estimated individuals per km^2) by its energetic conversion factor, then sum across all species to obtain DER. The resulting unit is therefore expressed in “moose equivalents per km^2” (although any of the four deer species could be used as the reference).

Because browsing impacts may show time lags, we preliminarily considered both recent-year (3-year or 5-year) and long-term (12-year) averages of DER and deer species densities. The long-term averages explained more variation in plant species richness and so were used in the final analyses. These averages were calculated for all deer combined (DER), as well as for each recorded species: moose, red deer, and small deer (where roe and fallow deer were combined). We decided to use five as the conversion factor between moose and ‘small deer’ rather than the average between fallow deer and roe deer when calculating DER, as the fallow deer harvest was much higher than the roe deer harvest in the area (Table 1), and previous DNA-analyses showed a comparable pattern of fallow deer dominating (Spitzer et al., 2019).

2.5. *Field-layer plant survey and vertical gap fraction estimation*

Vegetation surveys were carried out in 325 concentric plots of 10 m^2 (radius = 1.78 m, Fig. 1d) located in forests and forest edges. Most of the vegetation survey plots were in intermediate-aged stands (136) with the rest distributed between mature (46), young (30), sparse/low-productivity (27), clearcut stands (22), and other/unclassified (64). Qualified surveyors identified and recorded all vascular plant species as well as mosses, though lichens were not included. Unidentified bryophytes were collected as voucher specimens for later identification in the laboratory.

We use the term *field-layer* plant community to refer to the ground and near-ground vegetation consisting of bryophytes and vascular plants, including dwarf shrubs, forbs, graminoids and ferns, but excluding tree seedlings taller than 30 cm and lichens. Accordingly, only tree seedlings shorter than 30 cm were recorded, as taller individuals were considered belonging to the shrub or tree layer. No height restrictions were applied to other functional groups as they occur entirely within the field-layer.

Coverage of each species was assessed using the Braun-Blanquet (1932) cover-abundance scale, where species were assigned a score based on their estimated cover: 0 = present but < 1 % cover; 1 = 1–5 % cover; 2 = 6–25 % cover; 3 = 26–50 % cover; 4 = 51–75 % cover; and 5 = 76–100 % cover. Each species was also classified into one of seven functional/life-history groups: clubmosses, dwarf shrubs, ferns, forbs, graminoids, mosses or tree seedlings (see supplementary material). Here, ‘dwarf shrubs’ refers to low growing, woody species such as *Calluna*, *Empetrum*, and *Vaccinium*. We also included *Rubus spp.* in this group to reflect their perennial woody growth habit, despite their sometimes herb-like ecology.

In addition to plant community composition, we visually scored browsing on bilberry (*Vaccinium myrtillus*) at each plot. Browsing was estimated as the proportion of current year bilberry shoots that showed clear bite marks, assessed within the same 10 m^2 vegetation plot. As bilberry forms dense clonal mats, browsing was scored at the shoot level rather than individual. Each plot was assigned to one of six percentage categories, depending on the proportion of stems browsed (0 %, 1–10 %, 11–25 %, 26–50 %, 51–75 %, >76 %).

We also quantified understorey structural openness, using digital cover photography (DCP) to generate estimates via vertical gap fraction analysis. At each vegetation survey plot, vertical images (single field of view) were taken at 1 m above ground level using the front-facing camera (QCOM-AAQCAM-AA) from a Handheld Nautiz X6 set to automatic exposure. The images were batch-processed using Hemispherical_2.0 for ImageJ (Beckschäfer, 2015) to calculate vertical gap fraction. Digital cover photography was chosen over hemispherical photography as it was less cumbersome in the field whilst still capturing detailed vertical canopy gaps. This metric reflects the density of vegetation above 1 m, including tall shrubs and small trees, and captures the vegetation strata most directly utilised for cervid browsing (Spitzer et al., 2023, 2021). We use ‘vertical gap fraction’ throughout to avoid confusion with overstory canopy measurements.

3. Data-analysis

3.1. *Plant species richness and the intermediate disturbance hypothesis*

As a preliminary test, we assessed whether realised browsing pressure reflected deer density by modelling the proportion of bilberry browsed with beta regressions via the *betareg* package (Zeileis et al., 2004), with DER, and densities of moose, red deer and small deer as separate predictors. Proportions were adjusted using the Smithson–Verkuilen transformation (Smithson and Verkuilen, 2006) to fall within in the range (0,1) required for this analysis.

To model variation in species richness we fitted generalised linear models (GLMs) using negative binomial error distributions and a log link using the MASS package (Ripley and Venables, 2009) in R version 4.5.1 (R Core Team, 2025). For each browser group (DER, moose, red deer and small deer), functional group (forbs, graminoids, dwarf shrubs, and mosses), and vertical gap fraction, we specified two candidate models, a linear effect and a quadratic effect. Quadratic predictors were mean centred (mean = 0) before squaring to reduce collinearity and ease interpretation.

To account for the variation in sampling effort across tracts in terms of plots monitored (i.e. due to differences in landscape composition), the log-transformed number of plots sampled (hereafter log n plots) was included as a covariate, eliminating the need for rarefied or estimated species richness data. Forest stand characteristics were also accounted for by including the first principal component (PC1; here after *stand structure*) from a PCA based on the proportional area of logging classes within each tract (clearcuts, young forest, intermediate forest, mature forest, sparse/low productivity stands). PC1 captured a gradient separating structural extremes in stand types (clear cuts and mature forest) form intermediate developmental stages, reflecting differences in stand structure and disturbance history.

Model support was assessed with Akaike’s Information Criterion (AIC), where we considered the model with the lowest AIC as the best supported. Models with a ΔAIC ≤ 2 were considered as having comparable support and as such the simplest model was chosen. As a robustness check of non-linearity, we ran general additive models (GAMs) using the mgcv package (Wood, 2025) and inspected whether the smooth's effective degrees of freedom where either greater or less than 1 (evidence of non-linearity), verified whether the basis-dimension was adequate with gam.check, and compared the GAMs smooth shape to the shape of the appropriate GLM (e.g. direction and location of any humps) to assess whether the non-linear relationship was consistent. Smooth terms were estimated using thin-plate regression splines (bs = "tp"), with the basis dimension set at k = 7 and where the select = TRUE option allowed smooths to shrink towards linearity or zero where appropriate.

For all GLMs, residual checks were conducted with DHARMa (Hartig, 2016) and visualisations of predicted effects were produced using ggplot2 (Wickham et al., 2025) and ggeffects (Lüdecke, 2017).

3.2. *Indirect effects of browsers on vegetation structure and diversity*

In addition to species richness analyses, we assessed how vertical gap fraction and functional group cover (forbs, grasses, dwarf shrubs, and mosses) varies with changes in DER. These models were fitted using a beta regression via the *betareg* package (Zeileis et al., 2004). Similarly to previous analysis, two candidate GLMs (a linear effect and a quadratic effect) as well as a GAM were produced and were assessed with AIC. To meet the requirements of this analysis, cover variables were expressed as proportions and adjusted to fall strictly within the (0,1) interval, also using the Smithson–Verkuilen transformation.

We then applied structural equation modelling (SEM) using the *piecewiseSEM* package (Lefcheck et al., 2015) in R to test the direct and indirect effects of browsing on vegetation structure and species richness. Based on ecological theory, we specified a simplified path model in which browsing was modelled as a predictor of vegetation structure, specifically vertical gap fraction and the composition of the field layer functional groups, which in turn were specified as predictors of species richness. To reduce dimensionality and avoid multicollinearity among functional group cover variables, we conducted a principal component analysis (PCA) in R on dwarf shrub, graminoid, forb and moss cover. The first component (PC1; hereafter *vegetation gradient*) was retained and used as an integrative measure of vegetation composition in subsequent SEM analysis. Vertical gap fraction and vegetation gradient were modelled using linear models, as residuals were approximately normal. Species richness was modelled using a negative binomial generalized linear model to account for count data. Model fit was assessed using Shipley's D-separation tests and Fisher's C, which indicated adequate fit (C = 14.56, $df = 8$, $p = 0.068$). This piecewise approach avoids distribution assumptions required by covariance-based SEM and is well suited for relatively small samples (n = 33 tracts).

4. Results

4.1. *Deer density and proportion of bilberry browsed*

The percentage of bilberry browsed increased significantly with DER ($\beta = 0.0200 \pm 0.0071$, $z = 2.80$, $p = 0.005$) and small deer density ($\beta = 0.0051 \pm 0.0016$, $z = 3.20$, $p = 0.001$), with browsing percentage rising by about 2 % per additional DER and 0.5 % per additional small deer. In contrast, moose density alone and red deer density showed no relationship with bilberry browsing.

4.2. *Relationship between deer densities, browsing and plant species richness*

When deer were analysed by species/group, plant species richness showed significant associations with both small deer and moose density (Fig. 2a–b). The relationship between small deer density and field-layer richness was best described by a quadratic model (ΔAIC = 6.26 vs. linear) with a significant negative quadratic term ($\beta = -9.995 \times 10^{-6} \pm 4.37 \times 10^{-6}$, $z = -2.29$, $p = 0.022$) indicating a unimodal relationship, with plant species richness peaking at intermediate small deer densities. A GAM was used to confirm the shape of the relationship. This produced a curve of a similar shape, but the smooth term was non-significant (edf = 1.11, smooth $p = 0.167$). For moose, a linear GLM was favoured by parsimony (ΔAIC < 1) showing a decline in plant richness with increasing moose density ($\beta = -0.026 \pm 0.0084$, $z = -3.12$, $p = 0.0018$). The GAM provided better fit (ΔAIC = 4.59 vs, linear) with the smooth suggested some curvature to this relationship and revealing significant nonlinearity (edf = 3.04, smooth $p < 0.001$). Despite this curvature, the dominant pattern remained a negative association between plant species richness and moose density. No clear relationships with plant species richness were detected for deer energy requirement (DER) ($\beta = -0.0007 \pm 0.0024$, $z = -0.285$, $p = 0.776$) or for red deer density ($\beta = -0.0102 \pm 0.0072$, $z = -1.41$, $p = 0.16$). Across all models sampling effort (log n plots) was strongly positively related to species richness (all $p \leq 0.001$), while stand structure showed no significant association in any model (all $p > 0.05$).

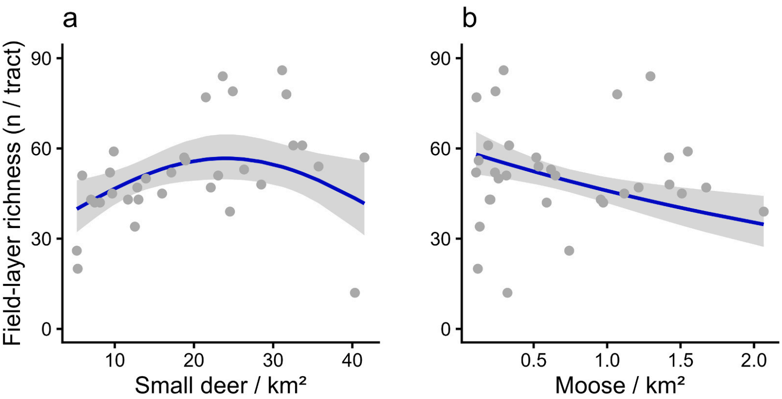

Fig. 2. The relationship between browser species/group and total plant species richness of the field-layer. Plots demonstrate (a) the relationship between field-layer richness and average small deer per km^2, and (b) the relationship between field-layer richness and average moose per km^2, as modelled by generalised linear models (GLMs). Points represent the average values per tract; the blue trend line represents the modelled fit and grey ribbons represent a 95 % confidence interval.

4.3. Relationship between browsing, vertical gap fraction and functional group cover

Average energy requirement (DER) was used to predict differences in vertical gap fraction and vegetation functional group cover via GLMs and GAMs. Vertical gap fraction increased with increasing DER, with a quadratic model best explaining this relationship ($\Delta AIC = 5.61$ vs. linear). The model had both a significant positive linear term ($\beta = 0.0114 \pm 0.0031$, $z = 3.63$, $p < 0.001$) and a negative quadratic term ($\beta = -4.40 \times 10^{-4} \pm 1.54 \times 10^{-4}$, $z = -2.86$, $p = 0.004$), where vertical gap fraction increased from low to intermediate DER and stayed high (Fig. 3a). A GAM produced a curve of similar shape (edf = 2.08, smooth $p < 0.001$), supporting this pattern but not improving upon the previous model ($\Delta AIC < 1$). Conversely, dwarf shrub cover declined with increasing DER, with a quadratic model also being preferred ($\Delta AIC = 5.24$ vs. linear). This model showed a negative linear effect ($\beta = -0.0156 \pm 0.0037$, $z = -4.21$, $p < 0.001$) with a positive quadratic term ($\beta = 5.20 \times 10^{-4} \pm 1.82 \times 10^{-4}$, $z = 2.86$, $p = 0.004$; Fig. 3b). The GAM revealed similar curvature (edf = 2.28, smooth $p < 0.001$) but did not meaningfully improve upon the quadratic GLM. Graminoid cover showed another pattern, with a unimodal humped relationship with DER (Fig. 3c). Here, a quadratic model was preferred ($\Delta AIC = 2.48$), with a positive linear term ($\beta = 0.0555 \pm 0.0252$, $z = 2.21$, $p = 0.027$) and a negative quadratic term ($\beta = -4.91 \times 10^{-4} \pm 2.36 \times 10^{-4}$, $z = -2.08$, $p = 0.038$). The GAM produced a curve of similar shape, though the smooth term was non-significant (edf = 1.17, smooth $p = 0.13$). Neither forb ($\beta = -0.0031 \pm 0.0051$, $z = -0.610$, $p = 0.542$) nor moss cover ($\beta = -0.0068 \pm 0.0040$, $z = -1.67$, $p = 0.094$) showed a discernible relationship with DER, with all tests showing no trend.

4.4. Relationship between vertical gap fraction, functional group cover and plant species richness

We used GLMs and GAMs to assess plant species richness as a function of each cover variable and gap fraction (Fig. 4). When vertical gap fraction was included as a predictor, a linear GLM best explained variation in species richness ($\Delta AIC = 1.52$ vs. quadratic, $\Delta AIC = 0.36$ vs. GAM) with species richness increasing with increasing vertical gap fraction ($\beta = 1.13 \pm 0.40$, $z = 2.86$, $p = 0.004$; Fig. 4a). Plant species richness was positively associated with graminoid cover ($\beta = 0.0164 \pm 0.0030$, $z = 5.51$, $p < 0.001$; Fig. 4b). A linear GLM provided the most parsimonious description of this relationship ($\Delta AIC = 1.30$ vs. quadratic), and although the GAM detected some curvature (edf = 3.37, $p < 0.001$), the overall pattern remained a strongly positive, roughly linear association. Species richness was also positively associated with stand structure in the linear GLM ($\beta = 0.0713 \pm 0.035$, $z = 2.037$, $p = 0.041$). Species richness initially appeared to show a non-linear relationship with forb cover, with a quadratic GLM providing the best fit when all tracts were included ($\Delta AIC = 19.11$ vs. linear, $\Delta AIC = 3.46$ vs.GAM). Richness increased with forb cover but displayed significant negative curvature (linear term: $\beta = 0.0399 \pm 0.0055$, $z = 7.28$, $p < 0.001$; quadratic term: $\beta = -0.0010 \pm 0.0002$, $z = -5.21$, $p < 0.001$), following a unimodal pattern. However, this curvature was strongly influenced by a single result from tract 12. When this tract was excluded a linear GLM provided the best fit, with species richness being positively associated with forb cover ($\beta = 0.0348 \pm 0.005$, $z = 6.97$, $p < 0.001$; Fig. 4c). Thus, the underlying positive linear relationship was consistent and robust to the exclusion of tract 12. Species richness showed no significant association with dwarf shrub ($\beta = -0.0078 \pm 0.0042$, $z = -1.73$, $p = 0.07$) nor with moss cover ($\beta = -0.0010 \pm 0.0034$, $z = -0.29$, $p = 0.78$) as there were no trends detected via GLM or GAM. In all models, sampling effort (log n plots) was positively associated with plant species richness (all $p < 0.001$), and apart from the graminoid model, stand structure was not significant in any other models (all $p > 0.05$).

4.5. Indirect pathways of browsing influence on plant richness

The first principal component (PC1) explained 41.9 % of the variation in functional group cover, with positive loadings for graminoids and forbs and negative loading for dwarf shrubs and moss. Higher PC1 scores therefore indicate communities dominated by graminoids and forbs as opposed to dwarf shrubs and mosses. We hereafter refer to this axis as vegetation gradient.

Structural equation modelling (Fig. 5) revealed that vertical gap fraction was positively associated with deer energy requirement (DER) ($\beta = 0.45$, $p = 0.009$). In turn, vertical gap fraction was positively associated with vegetation gradient (PC1; $\beta = 0.47$, $p = 0.012$) such that more open understories (with higher vertical gap fraction) were associated with greater graminoid and forb cover. Field-layer species richness was positively associated with vegetation gradient ($\beta = 0.46$, $p < 0.001$) indicating that communities composed mostly of graminoids and forbs supported higher species richness than those composed of dwarf shrubs and mosses. In addition to this indirect pathway, DER also had a significant direct negative effect on species richness ($\beta = -0.25$, $p = 0.029$). Together these coefficients indicate field-layer species richness is indirectly positively associated with DER via increased vertical gap fraction and a shift towards graminoid/forb-dominated communities. Stand structure had a significant positive effect on species richness within the SEM (PC1; $\beta = 0.30$, $p = 0.008$), whereas DER showed no significant direct relationship with vegetation gradient ($\beta = 0.11$, $p = 0.516$). As with all previous models, sampling effort (log n plots) remained a strong positive predictor of richness ($\beta = 0.81$, $p < 0.001$). The model explained 89 % of the variance in species richness (Nagelkerke $R^2 = 0.89$), 20 % in vertical gap fraction ($R^2 = 0.20$), and 28 % in vegetation gradient ($R^2 = 0.28$).

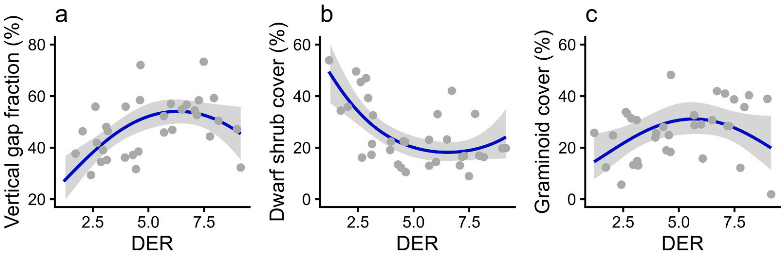

Fig. 3. The relationship between deer energy requirement (DER) and vertical gap fraction (a), dwarf shrub cover (b), graminoid cover (c) as modelled by generalised linear models (GLMs). Points represent the average values per tract; the blue trend line represents the modelled fit and grey ribbons represent a 95 % confidence interval.

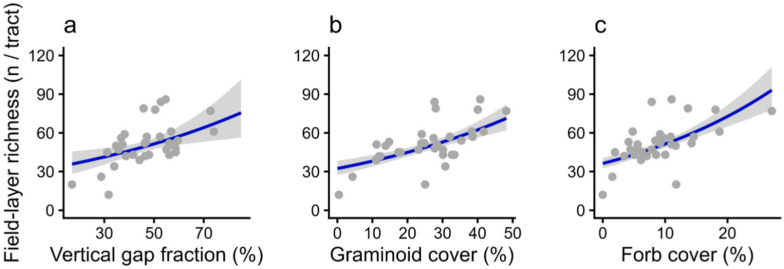

Fig. 4. The relationships between total field-layer plant species richness and average vertical gap fraction (a), average graminoid cover (b) and average forb cover (c) as modelled by generalised linear models (GLMs). Points represent the average values per tract; the blue line represents the modelled fit and the grey ribbons represent a 95 % confidence interval.

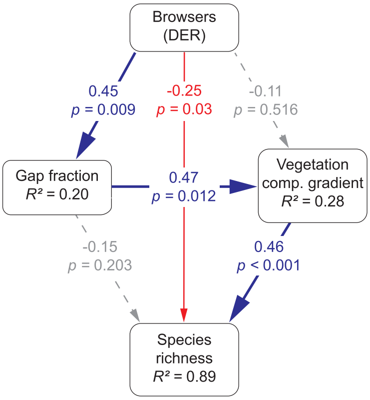

Fig. 5. Structural equation model of deer energetic requirement (DER), vegetation composition gradient, and plant species richness. Solid arrows denote significant paths ($p < 0.05$), with blue arrows indicating positive relationship and red arrows indicating negative. Dashed grey arrows denote non-significant paths. Numbers within arrows represent standardised estimates and significance level. R^2 values shown within boxes indicate the variance explained for each response variable; for species richness these represent Nagelkerke R^2 values. Neither sampling effort (log n plots) nor stand structure (PC1) were shown in the figure for clarity.

5. Discussion

Our results show a unimodal relationship between the density of the dominant group of browsers and plant species richness, with species richness peaking at intermediate small deer densities before declining at higher levels. The analyses suggest that browsing may increase vertical gap fraction and thereby change plant community composition, and that these structural changes are associated with increased species richness. Our results suggest that the primary influence of browsing on biodiversity is indirect, mediated by changing vegetation structure.

Scores for browsing on bilberry increased with small deer density and DER, confirming that higher deer densities are associated with more browsing. Thus, the observed unimodal response lends support to the Intermediate Disturbance Hypothesis (IDH), which proposes that moderate levels of disturbance maximise diversity by reducing the dominance of competitive species without causing extensive mortality or resource depletion (Connell, 1978; Gao and Carmel, 2020). While the IDH has been influential in grassland and savanna ecology, its application in boreonemoral forests remains under-explored, despite increasing evidence of disturbance-mediated diversity patterns in these ecosystems (Gill and Beardall, 2001; Schwegmann et al., 2025; Trepel et al., 2025). Our findings offer empirical support for the IDH in a boreonemoral context and suggests that browsing by deer may generate the disturbances that promote maximum species richness in vascular plants.

Interestingly, field-layer plant richness differed markedly in its associations with different browser species. While plant species richness exhibited a unimodal relationship small deer, moose showed a negative association. This divergence may reflect differences in dietary requirements, body size, and impact intensity due to differences in population densities. Moose, as large-bodied concentrate selectors, likely consume a broader range of woody species and produce coarse, patchier disturbances that may reduce structural complexity without necessarily promoting herbaceous growth (Edenius et al., 2002; Pastor et al., 1988; Suominen and Danell, 2006). Moose may also choose to spend more time in homogeneous, dwarf shrub dense forest patches, where the plant species richness is lower, as these habitats are full of their preferred forage (Hjeljord et al., 1990; Spitzer et al., 2021). By contrast, small deer may create more fine-scaled, heterogeneous disturbances that can support higher local richness, at least up to a threshold of browsing intensity (e.g. Schwegmann et al. 2023). These species-specific effects highlight the importance of browser community composition in shaping biodiversity outcomes and caution against generalisations based on overall browsing pressure alone (e.g. Speed et al. 2014).

Browsing and grazing appeared to influence field-layer plant diversity primarily through modifications in vegetation structure. Specifically, higher DER was associated with increased vertical gap fraction, which in turn was linked to a shift in vegetation composition from dwarf shrub and moss dominance towards graminoids and forbs. This indirect pathway corresponded with higher field-layer species richness and appeared to outweigh the weak negative direct association between DER and richness. Thus, browsing may modify competitive dynamics and resource availability in forests, most likely by creating structurally open conditions that favour light-demanding herbaceous species (Faison et al., 2016a; Ramirez et al., 2019; Chevaux et al., 2022). These mechanisms may create a mosaic of different habitats across different spatial and temporal scales, in what otherwise would be a more uniform, closed canopy forest with less variation in habitats. Our results support the view of browsing deer acting as ecosystem engineers, reshaping forest understories and altering the structural conditions under which biodiversity is maintained, consistent with intermediate disturbance dynamics.

While our findings provide strong support for the hypothesis that deer browsing influences biotic and abiotic conditions in the field layer, several limitations should be considered. Firstly, our analysis is based on observational data, which limits causal inference despite the use of piecewise structural equation modelling. Thus, a purely “bottom-up” mechanism, whereby deer preferentially occupy species-rich sites, cannot be completely excluded. However, several patterns argue against this interpretation. Species richness peaked at intermediate deer densities (rather than increasing monotonically), bilberry browsing increased with long-term deer density (indicating realised top-down pressure), and 12-year average deer density was a better predictor of plant richness than current year density. Secondly, our use of combined deer energy requirement (DER) index inevitably simplifies true variation in browsing pressure. Individual energy needs differ with age, sex, behaviour, etc. and these sources of variation are not captured in our conversion factors. In mixed-species communities, differing diets and foraging strategies further broaden the range of browsing impacts. Thus, whilst using a composite DER index may be useful for reducing the number of factors entered in statistical models, it may also remove components crucial for understanding the relationship with biodiversity. Resolving these individual-level differences would require DNA-based identification of pellet producers, which is prohibitively costly at the spatial scale of this study. Thirdly, part of the observed variation in species richness and plant community structure could instead reflect the effects of rotation forestry, where stands move through successional stages and deer distribute themselves according to resource availability. However, as stand structure was not a significant predictor of species richness in all but one of our models, forestry effects are unlikely to fully explain the results. Finally, we combined long-term data on deer densities with snapshots on species richness and vegetation structure from the summer in a single year. Both vegetation structure and species occurrence will be affected by the conditions in previous years, and our analyses provided stronger relationships when we used average deer densities across all years as compared to limiting ourselves to recent years only. Nevertheless, we may miss lagged responses and may be unable to pick up seasonal dynamics. These limitations highlight the need for complementary experimental or high-resolution temporal studies to validate and refine the patterns observed here.

Taken as a whole, our findings highlight the complexity of herbivore–plant interactions in boreonemoral forests and emphasise the need to account for browser identity, local density, as well as spatial and temporal variability when assessing and predicting biodiversity outcomes. Moderate, varied browsing can enhance species richness by reducing structural dominance and facilitating herbaceous growth. These insights have important implications for integrated forest and wildlife management, suggesting that biodiversity goals may be best supported not by uniformly reducing deer numbers, but by managing for a diverse and spatially heterogeneous browser community and browsing pressure. This approach may help reconcile competing objectives in forest landscapes where timber production, game management, and conservation co-occur.

CRediT authorship contribution statement

Fredrik Widemo: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anne-Maarit Hekkala:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Formal analysis, Conceptualization. **Joseph John Anderson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used ChatGPT (Open AI) in order to receive support in troubleshooting and refining R code for data analysis. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article. These tools were not used in any other aspect of preparing this work.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123422.

Data Availability

Data will be made available on request.

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Supplementary material

List of species recorded per tract and the corresponding functional group classification

		Tract																														
Species	Functional group	1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Achillea millefolium	Forb	x						x		x				x		x	x			x		x											x	
Achillea ptarmica	Forb	x																						x										
Agrostis canina	Graminoid																								x									
Agrostis capillaris	Graminoid	x																																
Ajuga pyramidalis	Forb															x																		
Alchemilla vulgaris	Forb										x								x															
Alnus glutinosa	Tree sapling																					x								x				
Alopecurus pratensis	Graminoid																					x		x				x						
Anemone nemorosa	Forb	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x	x	x		x	x
Angelica sylvestris	Forb																							x										
Anomodon longifolius	Moss																					x		x										
Anthoxanthum odoratum	Graminoid	x	x		x										x	x				x			x	x								x	x	x
Anthriscus sylvestris	Forb		x											x										x				x						
Arrhenatherum elatius	Graminoid	x	x					x						x	x	x			x	x		x	x	x	x	x			x				x	
Athyrium filix femina	Ferns	x		x	x		x	x	x	x				x	x				x			x	x	x	x			x		x		x		
Aulacomnium palustre	Moss		x							x								x			x											x		x
Avenula pubescens	Graminoid																																	
Betula pendula	Tree sapling	x		x				x	x		x	x		x	x	x		x	x	x		x	x	x	x				x	x		x	x	
Betula pubescens	Tree sapling	x					x	x	x					x	x							x			x					x				x
Briza media	Graminoid															x							x											
Calamagrostis arundinacea	Graminoid	x		x				x	x	x	x	x	x	x	x			x		x	x	x	x	x	x	x				x				
Calamagrostis epigejos	Graminoid																x																	
Calamagrostis purpurea	Graminoid	x			x			x						x								x		x				x	x	x				
Calluna vulgaris	Dwarf shrub		x	x	x	x			x	x	x	x		x	x	x		x	x	x	x		x		x	x	x	x	x		x	x	x	x
Campanula glomerata	Forb										x																							
Campanula patula	Forb																											x						
Campanula persicifolia	Forb		x																									x						
Campanula rotundifolia	Forb	x		x	x			x		x														x									x	x
Carex acuta	Graminoid																																	
Carex brunnescens	Graminoid																																	
Carex canescens	Graminoid							x																			x				x			
Carex capillaris	Graminoid																x																	
Carex digitata	Graminoid	x		x	x			x				x	x						x			x									x		x	

		Tract																																
Species	Functional group	1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Carex echinata	Graminoid	x	x						x					x	x				x				x							x				
Carex hirta	Graminoid																					x												
Carex limosa	Graminoid																															x		
Carex nigra	Graminoid		x					x	x	x		x		x	x	x		x	x															
Carex ovalis	Graminoid	x						x	x			x		x					x	x		x	x	x				x						
Carex pallescens	Graminoid	x		x					x	x		x	x	x	x	x		x		x		x	x			x					x			x
Carex panicea	Graminoid	x			x				x	x	x	x		x	x		x		x				x			x	x		x	x	x	x	x	x
Carex pilulifera	Graminoid																																	
Carex rostrata	Graminoid													x																				
Carex spicata	Graminoid							x														x												
Carex vesicaria	Graminoid																											x			x			
Cerastium fontanum	Forb							x	x			x										x	x		x		x							x
Ceratodon purpureus	Moss							x									x											x						
Chamaenerion angustifolium	Forb																						x							x				
Cirsium arvense	Forb				x									x					x	x		x						x					x	
Cirsium palustre	Forb				x						x	x	x											x						x		x		
Cirsium vulgare	Forb																	x																
Convallaria majalis	Forb	x								x	x	x	x			x		x				x			x	x		x			x			
Corylus avellana	Tree sapling																					x												
Crepis paludosa	Forb																															x		
Cystopteris fragilis	Ferns																x						x					x						
Dactylis glomerata	Graminoid		x		x		x	x		x									x	x		x	x											x
Dactylorhiza maculata	Forb		x																															
Deschampsia cespitosa	Graminoid	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x
Deschampsia flexuosa	Graminoid	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Dicranum majus	Moss	x	x		x		x	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x	x	x		x	x	x	x	
Dicranum polysetum	Moss	x	x	x				x	x	x	x	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Dicranum scoparium	Moss	x	x	x	x	x	x	x	x	x	x		x		x			x		x		x	x	x	x	x	x	x	x	x		x		x
Dicranum spp.	Moss																											x						
Digitalis purpurea	Forb							x																										x
Dryopteris filix mas	Ferns											x	x									x	x	x			x							x
Elymus caninus	Graminoid																																	
Elytrigia repens	Graminoid																					x		x										
Empetrum nigrum	Dwarf shrub			x																														
Epilobium collinum	Forb																										x					x		
Equisetum arvense	Horsetails																		x					x				x						
Equisetum palustre	Horsetails																														x			

		Tract																																
Species	Functional group	1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Equisetum sylvaticum	Horsetails	x		x		x					x	x	x	x				x	x				x	x	x			x		x				
Eriophorum vaginatum	Graminoid																												x					
Festuca ovina	Graminoid						x																											
Filipendula ulmaria	Forb						x												x			x		x				x						
Filipendula vulgaris	Forb		x																				x					x	x					
Fragaria vesca	Forb	x	x	x	x	x						x	x			x	x	x	x	x			x					x		x	x	x		x
Fraxinus excelsior	Tree sapling																																	
Galeopsis tetrahit	Forb																											x	x		x			
Galium album	Forb			x	x					x			x										x											
Galium boreale	Forb	x							x													x	x	x				x		x			x	x
Galium spurium	Forb	x									x											x		x				x						
Galium suecicum	Forb																																	
Galium verum	Forb													x		x				x			x	x				x	x				x	x
Geranium robertianum	Forb																																	
Geranium sylvaticum	Forb															x	x					x						x						
Geum rivale	Forb						x						x						x					x										
Glechoma hederacea	Forb																										x	x			x			x
Gymnocarpium dryopteris	Ferns							x	x						x		x											x						
Helianthemum nummularium	Forb															x																		
Helictochloa pratensis	Graminoid	x												x				x						x				x	x	x				
Hepatica nobilis	Forb											x							x			x	x										x	
Hieracium sect. Hieracium	Forb	x			x				x	x		x	x	x	x	x		x	x				x	x	x	x		x		x	x	x	x	x
Hieracium umbellatum	Forb	x	x										x	x				x				x		x				x		x	x	x		x
Holcus lanatus	Graminoid																						x											
Hylocomium splendens	Moss	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Hylotelephium telephium	Forb																x																x	
Hypericum maculatum	Forb	x								x	x	x	x	x		x	x			x		x	x	x				x					x	
Hypericum perforatum	Forb		x																															
Hypnum cupressiforme	Moss			x				x		x		x		x	x							x		x		x		x		x				
Juncus articulatus	Graminoid																			x														
Juncus effusus	Graminoid	x			x			x	x			x		x	x			x	x	x		x	x	x	x	x	x	x		x		x		
Juniperus communis	Tree sapling														x			x	x					x										
Koeleria macrantha	Graminoid																						x					x						
Lactuca muralis	Forb	x					x				x	x		x	x	x	x	x	x			x	x	x	x			x	x	x	x		x	
Larix decidua	Tree sapling																					x												
Lathyrus linifolius	Forb	x			x	x				x	x	x	x		x				x	x		x	x					x	x		x	x	x	x
Lathyrus pratensis	Forb	x	x		x					x	x	x		x				x		x		x	x	x				x					x	x

		Tract																																
Species	Functional group	1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Lathyrus vernus	Forb																														x			
Leersia oryzoides	Graminoid																							x										
Leucanthemum vulgare	Forb		x							x				x						x			x											x
Leucobryum glaucum	Moss																		x													x		
Linnaea borealis	Forb															x																		x
Lolium perenne	Graminoid															x																		
Lotus corniculatus	Forb																					x												
Luzula luzuloides	Graminoid	x							x					x					x				x											
Luzula multiflora	Graminoid	x							x		x			x	x	x			x	x			x		x		x		x		x			x
Luzula pallescens	Graminoid			x																														
Luzula pilosa	Graminoid	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x		x	x	x	x	x	x	x	x
Lycopodium clavatum	Clubmoss																		x															
Lysimachia thyrsiflora	Forb																							x				x			x			
Lysimachia vulgaris	Forb																							x						x				
Lythrum salicaria	Forb																	x				x												
Maianthemum bifolium	Forb	x		x				x	x	x	x	x	x	x	x	x	x			x					x		x		x		x			x
Malva moschata	Forb																					x												
Marchantia polymorpha	Moss																					x												
Melampyrum sylvaticum	Forb				x			x	x		x		x	x		x	x	x		x		x	x		x		x	x	x			x	x	x
Melica nutans	Graminoid	x		x						x	x	x		x	x	x	x		x	x		x	x	x			x	x	x			x		x
Mentha arvensis	Forb																					x		x										
Menyanthes trifoliata	Forb		x																											x	x			
Milium effusum	Graminoid								x							x							x											
Mniaceae spp.	Moss														x			x				x	x					x			x			
Mnium hornum	Graminoid																								x									
Moehringia trinervia	Forb														x																			
Myosotis sylvatica	Forb																																x	
Orthilia secunda	Forb				x																													
Oxalis acetosella	Forb	x		x		x	x		x	x	x	x	x	x	x	x	x			x		x	x	x				x	x	x	x			x
Paris quadrifolia	Forb																x																	x
Petasites albus	Forb																											x						
Phleum pratense	Graminoid										x								x					x									x	
Phragmites australis	Graminoid																						x											
Picea abies	Tree sapling	x	x	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x		x	x		x	x	x	x	x
Pilosella cymosa ssp. cymosa	Forb															x																		
Pilosella officinarum	Forb	x																	x	x														
Pimpinella saxifraga	Forb		x							x				x		x			x	x														

Species	Functional group	Tract																																
		1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Pinguicula vulgaris	Forb																							x										
Pinus sylvestris	Tree sapling	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x
Plagiochila asplenioides	Moss	x	x	x																														
Plagiomnium affine	Moss									x						x	x					x										x		
Plagiomnium undulatum	Moss	x																																
Plagiothecium curvifolium laetum	Moss		x																											x				
Plantago lanceolata	Forb															x																		
Plantago major	Forb	x			x			x																x										
Pleurozium schreberi	Moss	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Poa annua	Graminoid													x									x					x						
Poa nemoralis	Graminoid				x		x																x					x						
Poa trivialis	Graminoid																							x	x									
Polygala vulgaris	Forb									x						x				x														
Polygonatum odoratum	Forb																					x												
Polypodium vulgare	Ferns	x																x				x				x								
Polytrichum commune	Moss	x	x	x	x			x	x	x	x						x								x			x	x	x	x	x	x	x
Polytrichum juniperinum	Moss			x						x						x																	x	x
Populus tremula	Tree sapling	x			x			x	x	x		x	x		x	x	x	x	x	x		x	x	x			x	x				x	x	x
Potentilla argentea	Forb	x																					x											
Potentilla erecta	Forb	x	x	x	x		x		x					x	x		x			x			x	x	x		x	x	x		x			x
Potentilla palustris	Forb		x																											x	x			
Primula veris	Forb		x																															
Prunella vulgaris	Forb	x			x			x														x												
Prunus avium	Tree sapling																																	
Pteridium aquilinum	Ferns	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Ptilium crista-castrensis	Moss																					x								x			x	
Pyrola rotundifolia	Forb																x																	
Quercus robur	Tree sapling			x	x	x	x		x				x		x	x	x	x	x	x		x	x	x	x	x	x	x	x		x		x	x
Racomitrium lanuginosum	Moss															x																		
Ranunculus acris	Forb	x	x							x	x		x			x		x	x	x		x	x	x	x			x					x	
Ranunculus auricomus	Forb						x																					x						
Ranunculus flammula	Forb	x												x																				
Ranunculus lingua	Forb																											x						
Ranunculus repens	Forb	x		x	x			x				x						x		x		x		x				x		x				
Rhododendron tomentosum	Dwarf shrub																												x					
Rhynchospora alba	Graminoid		x																															

Species	Functional group	Tract																																
		1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Rhytidiadelphus squarrosus	Moss																	x																
Rhytidiadelphus triquetrus	Moss	x		x		x			x	x		x	x						x			x	x			x							x	
Ribes nigrum	Dwarf shrub																																	
Rosa dumalis	Dwarf shrub																										x							
Rubus fruticosus	Dwarf shrub																							x			x							
Rubus idaeus	Dwarf shrub	x	x	x	x		x	x		x	x	x	x		x	x	x	x	x	x		x	x	x	x		x	x	x	x	x		x	x
Rubus saxatilis	Dwarf shrub	x											x						x															
Rumex acetosa	Forb							x												x			x	x									x	
Rumex acetosella	Forb							x	x	x										x		x												
Rumex crispus	Forb												x									x												
Salix caprea	Tree sapling	x			x		x			x	x	x			x		x		x				x	x						x			x	x
Salix cinerea	Tree sapling				x				x					x										x								x		
Sambucus racemosa	Dwarf shrub						x																						x					
Scirpus sylvaticus	Graminoid																					x						x						
Scrophularia nodosa	Forb																											x						
Scutellaria galericulata	Forb																											x						
Senecio sylvaticus	Forb	x		x				x	x		x	x		x	x	x		x	x	x		x	x	x	x		x	x	x	x				x
Solidago virgaurea	Forb										x	x	x			x	x						x				x	x						
Sorbus aucuparia	Tree sapling	x	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x			x	x	x		x	x	x		x	x	x	
Sorbus intermedia	Tree sapling					x											x	x						x										
Sphagnum angustifolium	Moss																		x								x							x
Sphagnum capillifolium	Moss	x			x						x				x			x	x		x				x			x		x				
Sphagnum girgensohnii	Moss		x	x	x			x	x	x				x	x				x	x				x		x	x	x	x	x				x
Sphagnum squarrosum	Moss	x	x	x										x																x	x			
Stachys sylvatica	Forb						x				x					x	x					x		x	x									
Stellaria graminea	Forb	x			x					x	x	x	x	x	x				x	x		x	x	x				x				x	x	x
Stellaria media	Forb																																	
Taraxacum sect. ruderalia	Forb	x	x		x										x	x				x			x	x									x	
Trientalis europaea	Forb	x	x	x				x	x	x	x			x	x					x			x		x		x	x	x		x	x	x	x
Trifolium hybridum	Forb										x							x																
Trifolium medium	Forb	x								x		x		x	x			x		x			x	x				x					x	x
Trifolium pratense	Forb	x	x		x						x					x		x				x												
Trifolium repens	Forb	x												x		x		x				x		x								x		
Tripleurospermum perforatum	Forb																											x				x		
Tussilago farfara	Forb						x																											
Ulmus glabra	Tree sapling																					x												
Urtica dioica	Forb	x		x			x					x		x	x							x	x					x						

		Tract																																
Species	Functional group	1	3	5	7	9	12	14	16	18	20	22	24	25	27	29	30	31	33	34	35	36	37	38	39	41	42	44	45	46	47	48	49	50
Vaccinium myrtillus	Dwarf shrub	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Vaccinium oxycoccos	Dwarf shrub																												x					
Vaccinium uliginosum	Dwarf shrub									x																			x					
Vaccinium vitis idaea	Dwarf shrub	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Veronica beccabunga	Forb																											x						
Veronica chamaedrys	Forb		x							x					x	x				x		x	x	x				x	x	x			x	x
Veronica officinalis	Forb	x		x	x		x	x	x	x	x	x	x	x		x						x	x	x	x			x			x			
Veronica serpyllifolia	Forb															x	x			x		x	x		x							x	x	x
Vicia cracca	Forb				x					x	x	x				x		x	x			x												
Vicia sepium	Forb				x						x												x										x	
Vicia sylvatica	Forb		x													x	x					x												x
Viola palustris	Forb		x																			x		x										
Viola riviniana	Forb	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x		x	x	x	x