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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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ABSTRACT

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

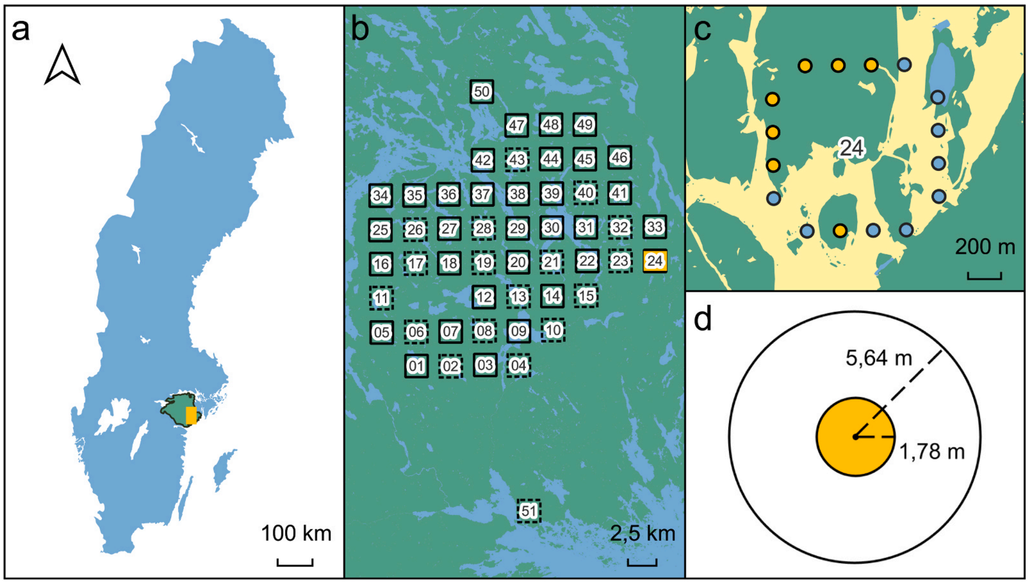

Fig. 1. The study area is located in southern Sweden (a) at the boreonemoral transition zone, the county of Södermanland is outlined and shown in green. The sampling was conducted using 1 × 1 km (perimeter 4 km) tracts (b), where sampling plots were systematically placed 200 m apart along the edge (c). 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 $\Delta AIC \leq 2$ 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 ($\Delta AIC = 6.26$ 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 ($\Delta AIC < 1$) 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 ($\Delta AIC = 4.59$ 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 $p > 0.05$).

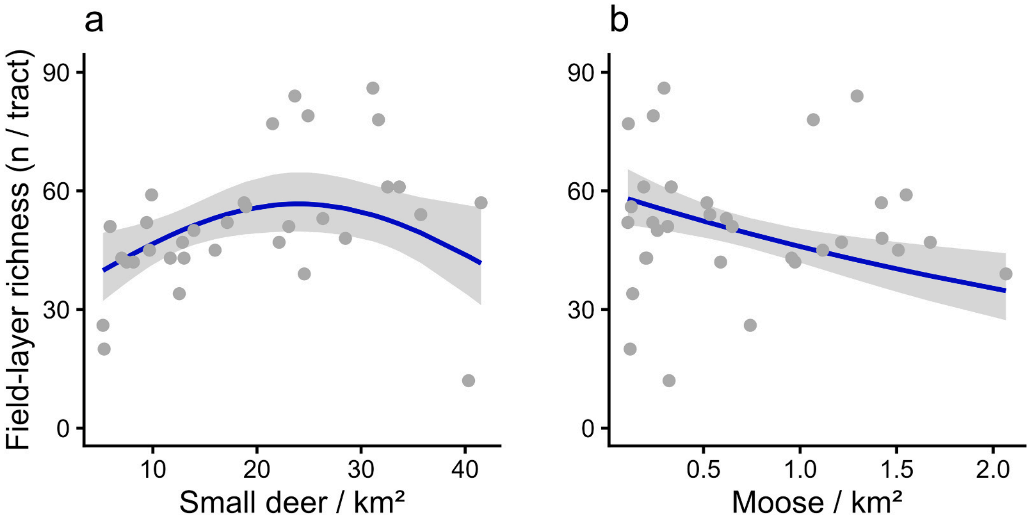

Fig. 2. The relationship between browser species/group and total plant species richness of the field-layer. Plots demonstrate (a) the relationship between field-layer richness and average small deer per km^2, and (b) the relationship between field-layer richness and average moose per km^2, as modelled 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 ($R^2 = 0.28$).

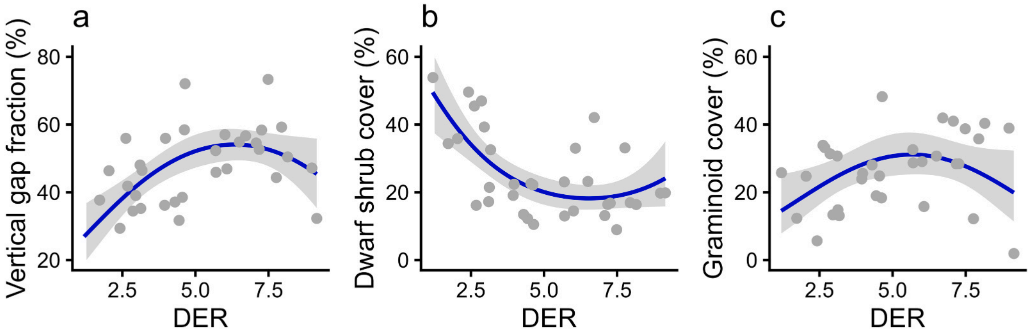

Fig. 3. The relationship between deer energy requirement (DER) and vertical gap fraction (a), dwarf shrub cover (b), graminoid cover (c) as modelled by generalised linear models (GLMs). Points represent the average values per tract; the blue trend line represents the modelled fit and grey ribbons represent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

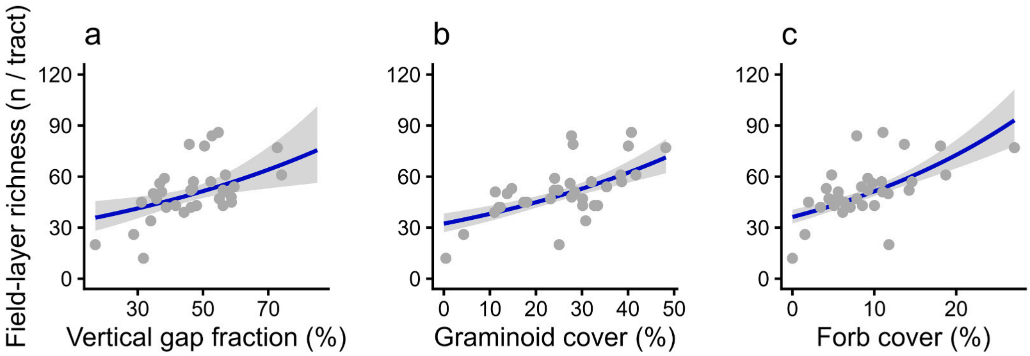

Fig. 4. The relationships between total field-layer plant species richness and average vertical gap fraction (a), average graminoid cover (b) and average forb cover (c) as modelled by generalised linear models (GLMs). Points represent the average values per tract; the blue line represents the modelled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

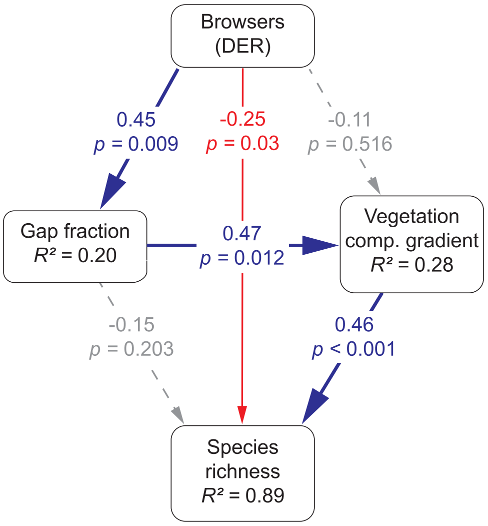

Fig. 5. Structural equation model of deer energetic requirement (DER), vegetation composition gradient, and plant species richness. Solid arrows denote significant paths ($p < 0.05$), with blue arrows indicating positive relationship and red arrows indicating negative. Dashed grey arrows denote non-significant 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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