

Research article

Benefit of the snout: wild boar rooting disturbance has downstream impacts on species diversity in local vascular plant communities

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ABSTRACT

Changes in land-use, climate and legislations, have shifted ungulate ranges throughout Europe. Ungulates can strongly impact local vegetation structure and composition, creating effects that can cascade throughout the ecosystem. Wild boar (*Sus scrofa*) may be particularly impactful as their feeding, nesting and rooting activities reduce plant cover and change local soil conditions. Quantifying these impacts is becoming increasingly important as wild boar continue to recolonize throughout Europe. In a comparative analysis, we investigated the short-term plant community response to wild boar rooting in a recently recolonised, boreal ecosystem. We explored how vascular plant species richness, diversity and the composition of species traits varied along a gradient of disturbance intensity over a 5-year period. We found higher overall vascular plant species richness and diversity with increasing rooting intensity. Plots with high-rooting intensity had, on average, 27 % more species diversity than plots in low-rooting intensity. Rooting intensity was also linked to a number of traits fundamental to interactions across trophic levels, including insect pollination, and nectar production. Importantly, we demonstrated that the ecological effects of rooting disturbance varied with forest stand age. In young forests, species richness was 61 % higher in high-intensity rooting plots than low-intensity rooting plot, however the effect reduced with stand age. This suggests that rooting and environmental conditions could have diverging impacts on different plants species. In a managed boreal forest, rooting by wild boar has the potential to alter local plant community composition, thereby shifting the local ecosystem, and potentially contributing to broader ecological community change.

1. Introduction

Environmental heterogeneity is regarded as one of the most important factors promoting species diversity (Bhattarai and Vetaas, 2003; Kreft and Jetz, 2007; Lundholm, 2009; Stein et al., 2014). Disturbances like fire and drought modify the physical environment, increasing spatial heterogeneity in light and soil resources (Bakker et al., 2003). This creates new niches that enhance biodiversity, as different plant species vary in their resource tolerance and utilization. Consequently, disturbances can allow greater species coexistence and result in communities with diverse physical and functional traits (Currie, 1991; Tews et al., 2004). The intermediate disturbance hypothesis (IDH) (Connell, 1978) suggests that species diversity is maximized at intermediate levels of disturbance. Intense or frequent disturbances may favour pioneer

species, while low disturbances benefit competitive species. Moderate levels of disturbances can allow for the coexistence of both, thereby enhancing diversity. However, disturbance-diversity relationships are complex and can be influenced by location conditions (Arnold, 1995; Mackey and Currie, 2001; Sousa, 1984), as well as the intensity and frequency of disturbance over time (Hall et al., 2012), and thus, the broad applicability of the IDH is under contention (e.g., Fox, 2013).

Plant characteristics and their ecological variation play a central role in maintaining species diversity. These traits directly influence how individual species respond to environmental change and different disturbance regimes. Interspecific trait variation leads to different survival strategies among coexisting species: disturbances that benefit one species (e.g., those with rapid growth rates), may disadvantage others with contrasting characteristics (e.g., stress-tolerant adaptations). This

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specialisation creates complementary ecological responses that buffer communities against stress and biodiversity loss, and maintain ecosystem functioning (Hooper and Vitousek, 1997; Isbell et al., 2011).

Large wild ungulates influence vegetation structure and composition in grasslands and forests (Pringle et al., 2023). Herbivory and seed dispersal can alter species distribution and affect nutrient cycles (Hobbs, 1996; Heinken et al., 2006; Barrios-Garcia and Ballari, 2012; Dovrat et al., 2012; Baltzinger et al., 2019). Activities such as rooting, grazing, trampling and wallowing reduce plant cover and change local soil conditions, potentially disrupting successional processes and causing cascading effects in the ecosystem (Hobbs, 1996; Barrios-Garcia and Ballari, 2012). Wild boar (*Sus scrofa*) is one of the most widely distributed ungulate species in Europe, as populations recolonize their native ranges from which they were once extirpated. In Sweden, wild boar numbers have increased rapidly in recent decades, now re-established in the southern and central parts of the country (Bergqvist et al., 2024). As ecosystem engineers (Vitousek, 1990; Jones et al., 1994; Crooks, 2002), wild boar impact vegetation cover, plant diversity, and regeneration through their rooting behaviour (Barrios-Garcia and Ballari, 2012), which can significantly alter the physical environment, influencing species dispersal and recruitment probabilities (Gómez, 2004). In forest systems with high wild boar populations, understorey cover can decrease by up to 80 % (Singer et al., 1984), potentially leading to reduced biological diversity and local extirpation of species (Singer et al., 1984; Gilliam, 2007; Gray et al., 2020). Contrastingly, soil disturbance caused by rooting activity may favour species that are disturbance-adapted, have short life spans and grow quickly (Dalling, 2008). The multifaceted interactions among trophic levels raise concerns about the downstream effects of wild boar rooting on other organism groups. However, the relationship between wild boar rooting activity and plant communities is not well described in the current literature.

Understorey plant species in managed boreal forests are influenced by forestry practices, climate and ecological processes (Nilsson and Wardle, 2005; Christiansen, 2022). Boreal forests often have a dense understorey of ericaceous dwarf shrubs, which are well adapted to post-disturbance conditions (Nilsson and Wardle, 2005; Mielke et al., 2022). In Scandinavia, the natural disturbance regime has been suppressed in recent times (Nilsson and Wardle, 2005), which may have

increased dominance of the understorey by a few species. Recolonization of wild boar in these managed boreal forests may reintroduce disturbance to this system, thereby altering the understorey. The goal of this study was to investigate the effect of disturbance caused by wild boar rooting activity on local plant species diversity and community composition in a managed boreal forest ecosystem, which was recently recolonised by wild boar. To do so, we conducted a comparative analysis of the response of local plant communities along a gradient of disturbance (wild boar rooting intensity) over a 5-year period. We aimed to understand i) impacts of wild boar rooting intensity on local vascular plant species diversity components, and ii) which plant species-specific traits that were promoted by rooting. We predicted that, in our study area, a relatively homogenous boreal forest landscape, wild boar impacts on the plant community would follow the IDH, in that, increases in wild boar rooting intensity would increase plant diversity to a threshold, after which the diversity would decrease. We expected disturbance-adapted pioneer species to be more common where rooting disturbance is high, and species with stronger competitive traits to be more common where rooting disturbance is low.

2. Material and methods

2.1. Study area

We surveyed vascular plant communities in the Grimsö Wildlife Research Area (59°72' N, 15°47' E), located within the southern boreal vegetation zone (Moen, 1998) in south-central Sweden (Fig. 1). Historically dominated by small-scale agricultural practices, this region underwent rapid afforestation in the 1950's, initiated by the large-scale introduction of clearcut forestry (Roberge et al., 2020). Forestry then became the central land use in the area and, today, forests are intensively managed by conventional forest practices, with an average rotation time between 60 and 80 years, depending on local stand conditions. Current practices normally involve clear-cutting, typically succeeded by reforestation by planting and 1–2 thinning operations before the final clear felling of the total stand (Bernes, 2011). This produces a heterogeneous landscape with a mosaic of stands of different ages, within a broader, relatively homogenous boreal forest.

The research area comprises 13,000 ha, covered mainly by

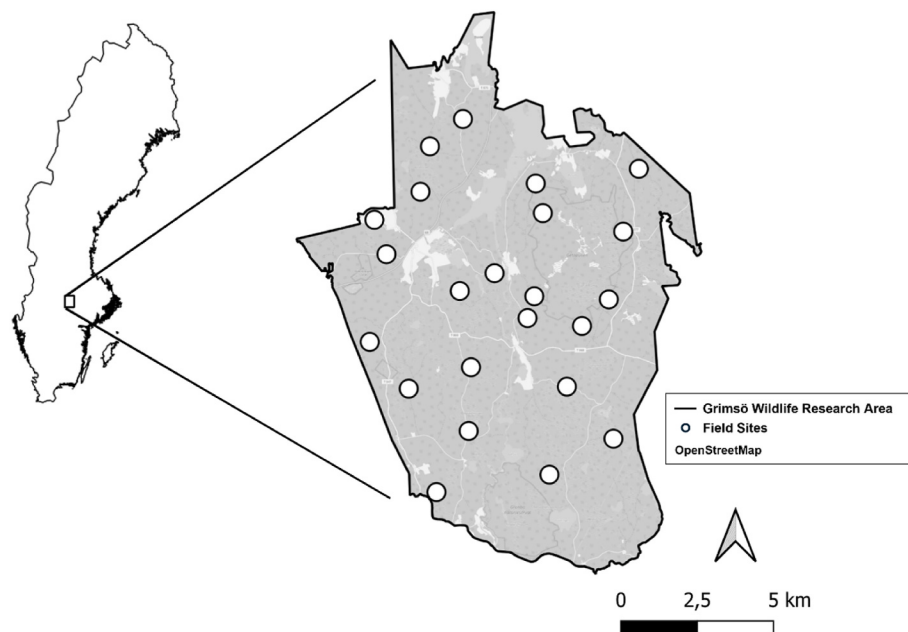


Fig. 1. Location of Grimsö Wildlife Research Area situated in south central Sweden (top left), and a zoomed-in panel of the study area (right) presenting the location of the 23 field sites of the experiment during 2018–2023.

intensively managed forest (74 %), dominated by two coniferous tree species (Norway spruce [*Picea abies*] and Scots pine [*Pinus sylvestris*]) and interspersed with low proportion (<10 %) of deciduous species such as silver birch (*Betula pendula*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*). The field layer consists mainly of dwarf shrubs (Guillet et al., 1996), dominated by bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*). For detailed information on all vascular plant species occurring within all sample plots in the study area, see Supporting information. The annual temperature in the area is 5–6 °C with a growing season (number of days with average temperature >5 °C) of 180–190 days. Average annual precipitation across the whole study area varies from 600 to 800 mm among years and the number of days with snow cover is 100–125 per year (WMO normal period 1991–2020; (SMHI, 2024)). The elevation of research area ranges 85–172 m a.s.l. Three ungulate species occur in the area: moose (*Alces alces*), roe deer (*Capreolus capreolus*), and wild boar. The wild boar has recently re-colonised the study area and the first known observation was in 2006 (SITES unpublished). All three ungulate species population sizes are controlled through hunting. Moose, and roe deer have stable populations over the Grimsö Wildlife Research Area, have estimated population densities of <1 moose/km² and <0.5 roe deer/km² (SITES, unpublished). The current population density of wild boar is not well known. However, according to surveys completed in 2024 (SITES, unpublished), it is expected to be about 0.49–0.66 individuals/km², making the wild boar density in the area very low compared to other areas in Sweden (Augustsson et al., 2024). Potential predators of wild boar wolf (*Canis lupus*) and lynx (*Lynx lynx*) constantly occur in the study area. One, or periodically two established wolf territories overlapped the entire study area throughout the study while lynx density is low and estimated to 0.65 animals/100/km² in the winter of 2024–2025 (Örebro County Board, <https://www.lansstyrelse.n.se/orebro/djur/jakt-och-vilt/stora-rovdjur.html>).

2.2. Experimental design and data collection

This study was conducted within a pre-existing framework of investigating the wider effects of supplemental feeding on local wild boar abundance and wild boar use of agricultural land. Between 2018 and 2023, we conducted a manipulative experiment in the Grimsö Wildlife Research Area, by introducing supplemental feeding sites in an area previously novel to feeding (see Supporting information). Supplemental feeding attracts wild boar to specific locations, providing an experimental method to manipulate local wild boar densities. This, in turn, increases the rooting intensity in those areas, creating a gradient of disturbance levels. This gradient can be used to examine changes in plant community composition. At 23 sites (with and without supplemental feeding), randomly selected within the study area, we repeatedly surveyed wild boar rooting intensity and plant communities in August to September (i.e., the end of the vegetation season) in 2018, 2020, 2022 and 2023. We conducted the vegetation survey in late summer because many plants are easier to identify once they have fully developed and new individuals have had time to germinate and mature. All sites were situated at least 745 m from one another (maximum distance, 2400 m). Each site was within the 13,000 ha research area, and thus had the same environmental conditions, such as elevation, soil condition, and historical and current land management. Given the even, stable distribution of moose and roe deer on the study area, we assumed their impact to be equal among the sites.

At each site, we sampled 12 10-m² circular plots. The sampling plots were located along longitudinal and latitudinal transects at distances 2, 10, 25, 50, 100 and 150 m from the centre of each site. In the cases of sites with supplemental feeding, the feeder served as the centroid, otherwise, the site centre as assumed from satellite and on the ground surveys. At each plot, we recorded: wild boar rooting intensity, all occurring plant species, plant coverage, forest age, and percentage deciduous trees. We visually estimated wild boar rooting intensity on an

ordinal scale, based on how much of the from above projected ground in the sample plot that was rooted i.e., the size of the exposed soil visible after the ground litter and top soil layer was removed by the boar: absent, low (<10 %), medium (10–50 %), and high (>50 %). Plant coverage for each plant species was visually estimated as one of four categories: absent, <10 %, 10–50 %, and >50 % within the 10-m² plot. To control for confounding effects of local habitat characteristics, we classified forest age into three categories, based on average tree height of trees occurring within 30 m of the plot: young (≤2 m), middle aged (2.1–15 m), and mature (>15 m). Finally, we estimated the percentage of deciduous trees (number of stems) within 30 m of the plot as whole integers from 1 to 100. No dependencies were found between rooting intensity and forest age (sites without supplemental feeding: Pearson $\chi^2 = 4.1167$, df = 4, p = 0.3904; sites with supplemental feeding: Pearson $\chi^2 = 9.5044$, df = 6, p = 0.1471; Supporting information), or between rooting intensity and percentage of deciduous trees (sites without supplemental feeding: Kruskal-Wallis $\chi^2 = 26.062$, df = 23, p = 0.2979; sites with supplemental feeding: Kruskal-Wallis $\chi^2 = 29.804$, df = 31, p = 0.5275). We only included survey plots in forests in the analysis (260 surveyed plots out of 276 total) and omitted plots in mires and meadows.

2.3. Ecological indicator and traits values

For a broader understanding of the impacts of wild boar rooting on plant communities and local biodiversity, we examined plant characteristics that determine responses to physical disturbance and effects on other species. We found no dissimilarity in the presence or absence of each plant species in plots of different rooting intensities (Analysis of Similarities statistic R = 0.1303, p < 0.001). Furthermore, the strongest association of a plant species to any rooting intensity was 0.43 (Indicator Species Association statistic ranging 0.129–0.43; Supporting information). Instead, we used species-specific ecological indicator values, physiological and reproductive traits, and conservation indices for vascular plant species of Sweden according to Tyler et al. (2021). To assess impacts of disturbance on plant communities, we included traits according to: life form – annual or long-lived perennial; response to disturbance – disturbance dependent or competitive; and seed properties – short-lived or long-lived seeds of the species. Moreover, to assess potential implications of wild boar rooting for other species groups, we included traits according to: pollinator dependence – pollinator independent or insect pollinated; biodiversity relevance – low or high; and nectar production – low or high (Table 1). Each plant species can have a unique combination of these 12 ecological traits (Supporting information). Limitations in sample size required the merging of two or more classes for several traits.

2.4. Statistical analysis

We investigated the effect of rooting intensity on overall vascular plant species richness (number of different plant species), species diversity (Shannon-Wiener index) and the count of species sampled that possess each of the ecological traits in the given plot, using generalised linear mixed models. To control for variation in environmental conditions we included at plot-level forest age (for simplicity was forest age roughly determined in the field by identifying three height classes, in these commercial forest plantation stands) and percentage deciduous trees (% of deciduous trees). To reduce skewness, percentage deciduous trees was log₁₀-transformed prior to the analyses, but because the log₁₀ of zero is undefined, we used a modification of the Smithson-Verkuilen transformation (Benítez-López et al., 2017) by adding half of the lowest non-zero values to all observations, i.e., 0.025, in our case. We applied a separate model to each response variable (species richness, species diversity or the count of species sampled that possess a certain ecological trait), including fixed effects of rooting intensity, forest age, percentage deciduous trees, and the interaction between rooting intensity and forest age, and rooting intensity and percentage deciduous trees. In the species

Table 1

List of ecological traits considered in the study and their corresponding trait category (and class) in the species list for vascular plant species of Sweden (Tyler et al., 2021). In the analysis, we use the count of species sampled, that possess each ecological trait in the given plot (e.g., count of species that are considered annual, i.e., species with strictly annual life form).

	Ecological trait	Definition	Category in Tyler et al., (2021)
Traits related to the impacts of disturbance on plant communities	Annual	Species with strictly annual life form	Longevity (class 1)
	Long-lived perennial	Species with long-lived perennial life form	Longevity (class 4)
	Disturbance dependent	Species that colonises already established vegetation and successfully competes with it	Soil disturbance (class 1)
	Competitive	Species that reproduces only in disturbed/naked soil or is not competitive in closed vegetation and requires soil disturbance at least every second year	Soil disturbance (class 6–9)
	Short-lived seeds	Species with transient or short-lived seeds (transient – 5 years)	Seed bank (class 1–2)
	Long-lived seeds	Species with long-lived or semipermanent seeds (>5 years)	Seed bank (class 3–4)
Traits related to interactions with other species groups	Pollinator independent	Species independent of pollinators	Pollinator dependence (class 0a–0c)
	Insect pollinated	Species exclusively pollinated by insects	Pollinator dependence (class 2a–2c)
	Low biodiversity relevance	Species with a low number of other organisms that depend on or utilise the species as food source (0–50 associated species)	Biodiversity relevance (class 1–4)
	High biodiversity relevance	Species with a modest to high number of other organisms that depend on or utilise the species as food source (>50 associated species)	Biodiversity relevance (class 5–8)
	Low nectar production	Species with no or small nectar production (0–5 g/m ² /year)	Nectar production (class 1–3)
	High nectar production	Species with modest to very large nectar production (>5 g/m ² /year)	Nectar production (class 4–7)

richness model and the ecological traits models, we used a Poisson error distribution, as the number of species are integers that cannot be negative, while in the species diversity model, we used Gaussian errors. Finally, we included a nested random effect term to the model consisting of plot ID within Year to control for temporal variation. We tested significant differences between categorical variables by comparing 95 % confidence interval (hereafter 95 % CI). We considered the effect of rooting on species richness, species diversity, or the incidence of a specific ecological trait to be significant, when these responses differed among rooting intensities, specifically between levels absent-medium, absent-high, and low-high. We chose to compare extremes, in order to avoid the masking of effects in consecutive levels of rooting intensity. Plants with incomplete identification in field protocols (only identified to the genus level; $n = 9$ taxa) were included in analyses of species richness and species diversity when no other species of that genus was represented in the plot, but removed from the ecological traits analyses since species within the genus have different ecological traits.

All statistical analyses were completed in R version 4.4.0 (R Core Team, 2024). The Shannon-Weiner index and Analysis of Similarities (ANOSIM) was computed using the R package *vegan* (Oksanen et al., 2018). Indicator species analysis was performed using the package *indicspecies* (De Cáceres and Legendre, 2009). Generalised linear mixed models were fitted using the package *glmmTMB* (Brooks et al., 2017). Confidence intervals (95 %) for the coefficients were derived using the *ggpredict()* function in *ggeffects* package (Lüdtke, 2018). Figures were created using the *ggeffects* package (Lüdtke, 2018) and tables using the package *sjPlot* (Lüdtke, 2021).

3. Results

3.1. Introduced artificial feeding

Overall, rooting intensity increased over the study period (Supporting information). The proportion of unrooted plots decreased from 89 % when the study was initiated (2018) to 67 % in 2022 and 69 % in 2023. By the end of the study, 7 % of the plots had high rooting levels compared to only 2 % in 2018. A similar pattern was demonstrated in plots with low rooting levels: increasing from 7 % of plots in 2018 to 15 % in 2023, and medium rooting levels: increasing from 2 % of plots in 2018 to 8 % in 2023. Moreover, intensified rooting was linked to the introduction of supplemental feeding (Supporting information). After feeding was initiated, rooting intensities were consistently higher in sites with supplemental feeding than in sites without supplemental feeding, and the differences decreased with distance to site.

3.2. Species richness and species diversity

Across all rooting intensity levels, we identified in total 185 vascular plant species (176 species to species level and 9 species to the genus level; Supporting information). As predicted, increased wild boar rooting intensity resulted in greater levels of plant species diversity, but only in young forest. We found no significant difference in species richness or species diversity in relation to rooting intensity in middle aged forest or mature forest (Fig. 2). To determine if rooting had a significant impact on richness and/or diversity, we compared these responses among non-consecutive rooting intensities, i.e., between levels absent-medium, absent-high, and low-high. Among comparisons, the most prominent differences in species richness were between rooting levels low-high, with an increase of on average 61 %, in young forest (Fig. 2). Similarly, lowest levels of species diversity were recorded in plots with low rooting intensity, with an increase of on average 27 % in plots with high rooting intensity. Both species richness and species diversity tended to increase in plots where the percentage of deciduous trees was high, particularly as rooting intensity increased (no effect of deciduous trees in plots with no rooting; Fig. 2).

3.3. Trait-specific responses

Rooting intensity was associated with a number of different ecological traits investigated in this study (Table 2). Four species: *Chenopodium album*, *Stellaria media*, *Poa annua* and *Polygonum aviculare*, possessed all ecological traits reportedly favoured by disturbance (Supporting information) and occurred more frequently in heavily rooted plots. In general, the count of species tended to increase in plots with a higher percentage of deciduous trees, particularly in rooted plots (Fig. 4, Table 2).

Species that were annual, disturbance dependent, or with long-lived seed bank, were positively influenced by rooting. The count of species sampled that possessed any of these traits was significantly higher in plots with medium or high rooting compared to plots with low or no (absent) rooting, in young forest (Fig. 3, Table 2). Plots with higher rooting disturbance tend to be less rich in competitive plant species and species with short-lived seed banks, compared to plots with no rooting

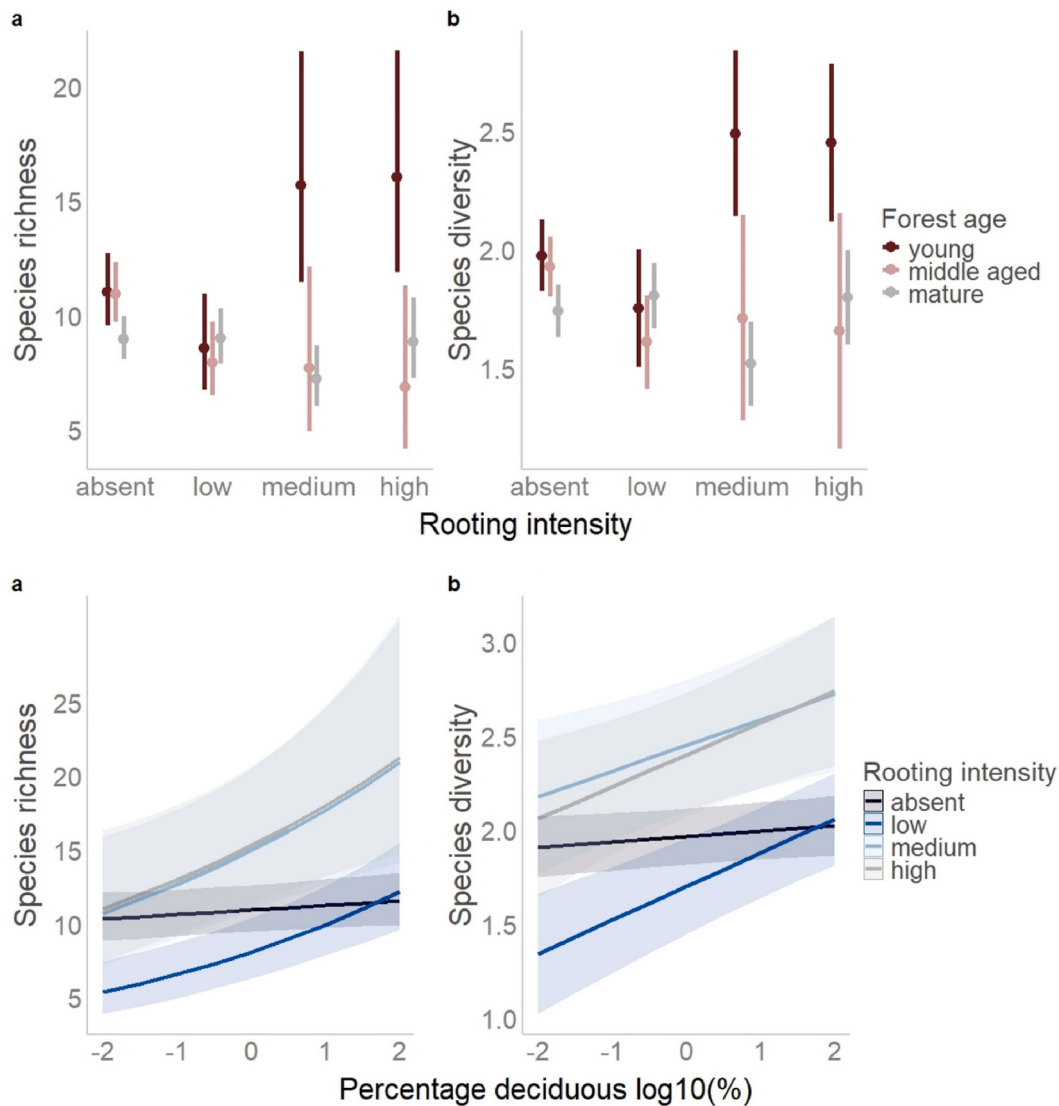


Fig. 2. Top: model predictions of species richness (number of species) (a) and species diversity (Shannon-Wiener index) (b) in 10-m² plots (n = 261) in relation to rooting intensity categories (absent, low: <10 %, medium: 10–50 %, high: >50 %) and forest age. Error bars represent 95 % confidence intervals. Colour indicated forest age: young (red), middle aged (rose), and mature (grey). Bottom: model predictions of species richness (a) and species diversity (b) in 10-m² plots (n = 261) in relation to rooting intensity categories (absent, low: <10 %, medium: 10–50 %, high: >50 %) and percentage deciduous trees in the plot. Shaded area represents 95 % confidence bands. Colour indicated rooting intensity: absent (black), low (dark blue), medium (light blue), and high (light grey).

but only in mature forest (Fig. 3, Table 2).

Species that were pollinator independent, of high biodiversity relevance, or with low nectar production were positively influenced by rooting. The count of species sampled that possessed any of these traits was significantly higher in plots with medium or high rooting compared to plots with low or no (absent) rooting, in young forest (Fig. 3, Table 2).

4. Discussion

Physical disturbance caused by wild boar rooting had an overall positive effect on local vascular plant species richness and species diversity in a managed boreal forest ecosystem, where wild boar are returning but not yet re-established. The effect of rooting was particularly pronounced in young forests and in areas with a high proportion of deciduous tree species, suggesting that a combination of disturbance mechanisms and local environmental conditions is important for plant diversity. Rooting does not affect all plant species in the same way, instead the response to rooting depends on each species' ecological traits. Thus, rooting disturbance by wild boar has the potential to alter

local plant community composition.

4.1. Species richness and species diversity

We showed that ungulate-facilitated changes, such as rooting by wild boar, can increase overall vascular plant species richness and diversity, at least in the short-term and at a local scale (Fig. 2). Rooting is generally reported to reduce species diversity (e.g., Bratton, 1975; Kotanen, 1995; Hone, 2002; Tierney and Cushman, 2006; Siemann et al., 2009; Pankova et al., 2020), with a few exceptions of positive (e.g., Van Leeuwen et al., 2025), or mixed results (e.g., Barrios-Garcia and Ballari, 2012; Parissi et al., 2014; Bongio et al., 2017; Pankova et al., 2020; Sütő et al., 2020; Van Leeuwen et al., 2025). The strength and shape of the top-down regulating forces influencing the plant community is likely mediated by the type of system in which they occur. In forest ecosystems, variation in understory vegetation communities and biodiversity depend on factors such as habitat type and local productivity (Hedwall et al., 2019; Hämäläinen et al., 2024). Many studies reporting a reduced plant diversity following wild boar rooting were conducted under warmer

Table 2

Overall summary of tested response variables and the direction of their relationship (+, −, 0) with rooting intensity, when controlling for forest age and percentage deciduous trees in close vicinity of the sample plot. When controlling for forest age, a significant response to rooting intensity for any response variable is indicated depending on the direction of the estimated response as increased (+), decreased (−) or when no response (0), when the responses differed among rooting intensities (non-overlapping 95 % CI), specifically between levels absent-medium, absent-high, and low-high. When controlling for percentage deciduous trees, the reported direction (+, −, 0) of the relationship reflects a significant coefficient ($p < 0.05$).

Response variable	Effect of rooting intensity in			Effect of percentage deciduous trees in			
	Young forest	Middle aged forest	Mature forest	Absent rooting	Low rooting intensity	Medium rooting intensity	High rooting intensity
Species richness	+	0	0	0	+	+	+
Species diversity	+	0	0	0	+	0	+
Species richness: Annual	+	0	+	0	+	+	+
Species richness: Long-lived perennial	0	0	0	0	+	+	+
Species richness: Disturbance dependent	+	0	+	0	+	0	0
Species richness: Competitive	0	0	−	0	+	0	0
Species richness: Short-lived seeds	0	0	−	+	+	0	0
Species richness: Long-lived seeds	+	0	+	+	+	0	+
Species richness: Pollinator independent	+	0	0	0	+	+	+
Species richness: Insect pollinated	0	0	0	0	+	+	+
Species richness: Low biodiversity relevance	0	0	0	0	+	+	+
Species richness: High biodiversity relevance	+	0	0	+	0	+	+
Species richness: Low nectar production	+	0	0	0	+	+	+
Species richness: High nectar production	0	0	0	+	+	0	0

climatic conditions (Kotanen, 1995; Hone, 2002; Tierney and Cushman, 2006; Siemann et al., 2009), or in areas of little or no forestry (Bratton, 1975; Hone, 2002; Siemann et al., 2009). In our study, however, we confirmed that rooting can lead to greater levels of vascular plant diversity in an intensively managed boreal forest with dense and even-aged stands. Thus, in homogeneous environment created by local forestry practices, e.g., short rotation times, rooting increases the environmental heterogeneity, and can be a benefit to local plant

communities. Future research into the environmental factors that mediate rooting-plant community relationships could provide valuable insights into the conditions under which rooting can be beneficial or detrimental.

In our study, the impact of rooting on plant diversity and richness was mediated by forest age, and the percentage of deciduous cover around a plot. Plant diversity and richness increased with rooting intensity in young forests but not in middle aged or mature forests (Fig. 2).

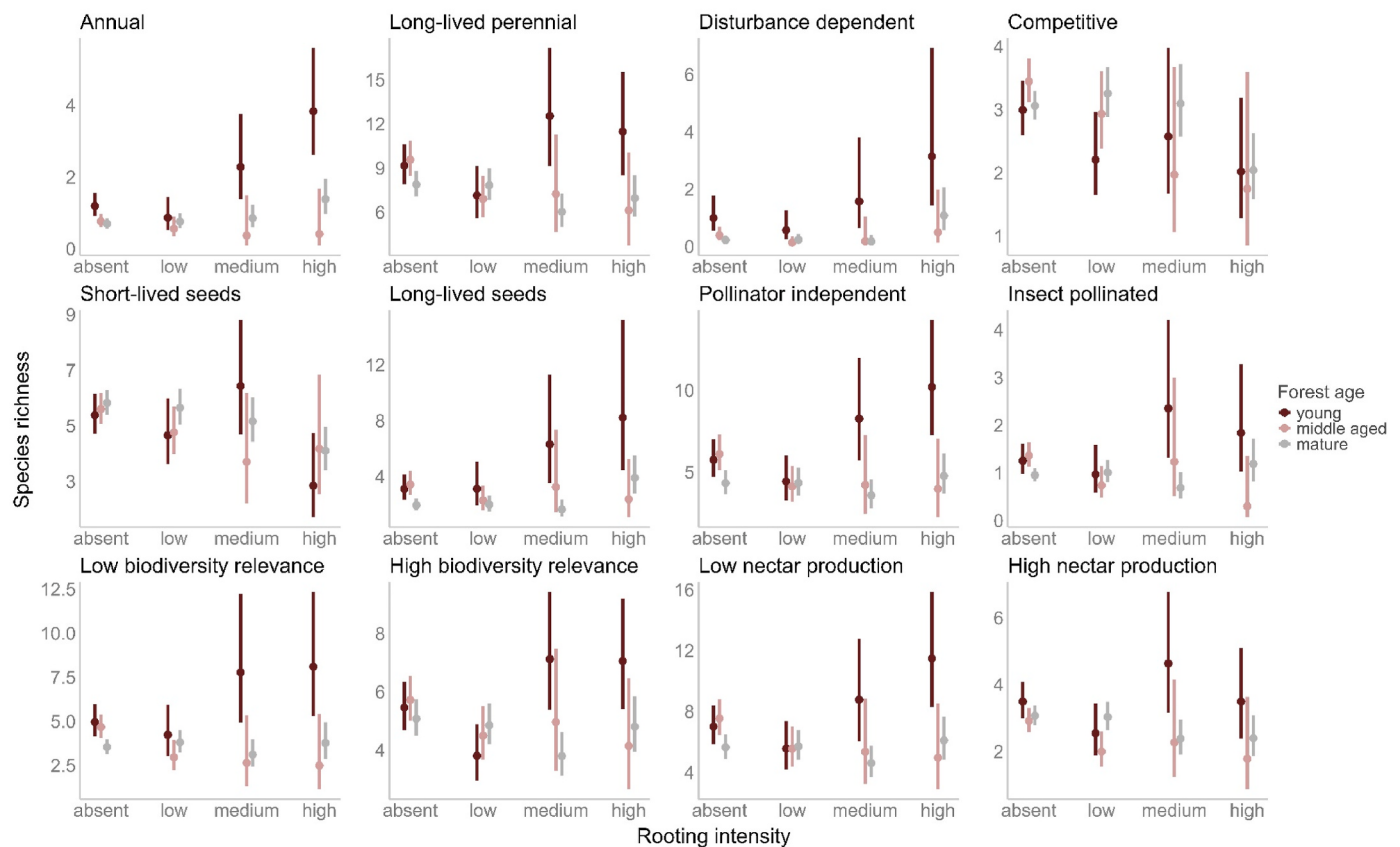


Fig. 3. Model predictions of species richness (number of species) of each ecological trait in 10-m² plots (n = 261) in relation to rooting intensity categories (absent, low: <10 %, medium: 10–50 %, high: >50 %) and forest age. Colour indicated forest age: young (dark red), middle aged (rose), and mature (light grey).

Furthermore, plant diversity and richness increased with the percent of deciduous tree cover, especially in medium and high-rooting intensity plots (Fig. 2). Since the 1950's, clearcutting and even-aged management has dominated Swedish forestry, resulting in denser, darker forests with decreased structural diversity and negative impacts on biodiversity (Hedwall et al. 2013, 2019; Hedwall and Brunet, 2016; Eyvindson et al., 2018; Svensson et al., 2019; Roberge et al., 2020). Light is a crucial resource for understorey plant diversity, and for the colonisation of new species (Bakker et al., 2003). Dense production forests, such as those in the present study, are often dominated by coniferous species and generally have poor light conditions (Lieffers and Stadt, 1994; Constabel and Lieffers, 1996). As forests age, light transmission decreases (Lieffers et al., 1999), impacting understorey diversity. We found that wild boar rooting can improve local conditions and plant diversity, potentially due to physical disturbance and soil turnover. However, rooting alone is not enough — light conditions are also vital, and as forests age, the lasting effects of rooting on diversity become uncertain. Although increased rooting in older stands could potentially counteract reduced light, we found no evidence of wild boar rooting preferences based on forest type (Supporting information). Since mixed forests with diverse tree species generally hosts more understorey species than forests with fewer tree species (Cavard et al., 2011), it may be useful to incorporating deciduous forests within production areas to counteract diversity loss (Felton et al., 2016).

4.2. Mechanisms promoting species diversity

Wild boar rooting not only affect plant diversity and richness in the affected area, but also have the potential to alter local plant community composition (Fig. 3). There is a complex relationship between wild boar disturbance and plant traits, with different species responding

differently based on their environmental requirements, tolerance limits, and resilience to disturbance. The intensity of rooting did not significantly affect the presence of specific species or the local species composition, and increased rooting intensity did not lead to more uniform plant communities or to communities dominated by a few generalist species. However, rooting did influence the overall trait composition of the plant community (Fig. 3). For example, we confirmed disturbance-adapted pioneer species to be more common under high disturbance, while species with stronger competitive traits decreased as rooting intensifies (Fig. 3), aligning with previous findings that disturbances favour stress-tolerant plants (Grime, 1979). We also found that seed properties were significantly related to rooting level, with species with long-lived seeds benefiting from rooting activities, while the effects on species with short-lived seeds were limited. Additionally, wild boar rooting increased the number of annual species by exposing soil for germination, supported by previous that link ungulate-induced disturbance to higher abundance of annual and biennial plants (Kotanen, 1995; Hayes and Holl, 2003; Li et al., 2024). Finally, we found a neutral relationship between rooting and number of long-lived perennials (Table 2), which may be explained by increased overall species richness masking directional effect on these species.

Despite its importance in the maintenance of many native-dominated ecosystems, wild boar rooting may also have undesirable consequences. One major concern is its potential to decrease native plants while promoting introduced species (Spear and Chown, 2009). Rooting disturbance may facilitate the establishment of invasive species, as shown by our findings that rooting intensity promote annual species (Fig. 3), which is a common trait of invasive species (Mathakutha et al., 2019). Additionally, studies indicate that soil disturbance by wild boar increases the abundance of exotic plant taxa (e.g., Singer et al., 1984; Tierney and Cushman, 2006; Siemann et al., 2009). While our research

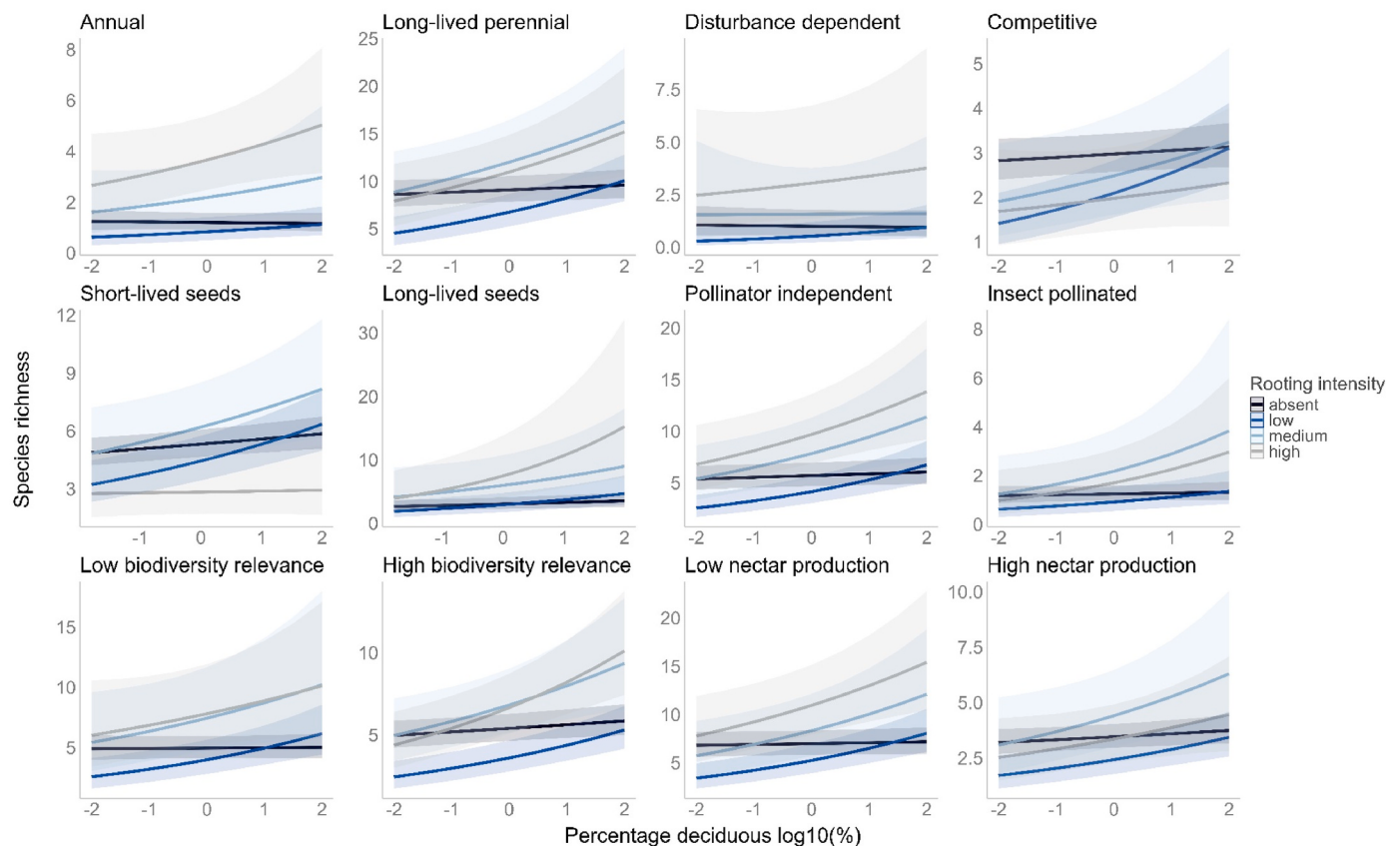


Fig. 4. Model predictions of species richness (number of species) of each ecological trait in 10-m² plots (n = 261) in relation to rooting intensity categories (absent, low: <10 %, medium: 10–50 %, high: >50 %) and percentage deciduous trees in the vicinity of the plot, with 95 % confidence intervals. Colour indicated rooting intensity: absent (black), low (dark blue), medium (light blue), and high (light grey).

did not focus on nativeness due to a low prevalence of non-native species (n = 16), propagation of non-native species is a potential negative impact of wild boar rooting on native plant communities, which deserves further research consideration.

Although the main mechanism for increasing plant species is the soil turnover and plant cover reduction, intensified animal traffic may contribute by facilitating seed dispersal, since animals carry seeds in their fur or faeces (Sorensen, 1986). Previous research has shown that artificial food provision can enhance local animal traffic and aggregation (Côté et al., 2004; Barrios-Garcia and Ballari, 2012; Pedersen et al., 2014). Although it was not the focus of our study, we observed in total 57 vertebrate species, excluding wild boar, at feeding sites, compared to in total 44 species at control sites (without feeding), supporting this trend (Augustsson et al. unpublished). If supplementary feeding is used to manage ungulate species, indirect impacts on plant communities should be investigated to catch any potential negative impacts.

4.3. Impacts in a larger context

The impacts of rooting disturbance on the plant community, may have cascading effects on higher trophic levels. For example, soil disturbance by wild boar rooting creates microclimates and local plant communities that support reproduction in rare butterflies, *Euphydryas aurinia* and *Melitaea aurelia*, in Germany (Scherer et al., 2025), and promotes nectar, larval host and egg-laying site resources for the Mediterranean endemic, *Zerynthia cassandra* (Labadessa and Ancillotto, 2023). These results indicate that wild boar may locally prove beneficial to endangered butterflies by favoring habitat quality and availability, and their role as ecosystem engineers should thus be further investigated to improve species and habitat management and conservation actions.

In our study area, rooting disturbance appears to promote species that are pollinator independent and those that have low nectar production (Fig. 3) which can impact pollinator visits and overall plant-pollinator interactions. Such changes in plant composition could potentially alter ecosystem function and services (Gilliam, 2007) and, consequently, modify structure and dynamics of entire ecosystems. However, with our trait-based approach, we were not able to distinctly categorize positive and negative downstream impacts. For example, while low nectar production plants were favoured, we also found that rooting promoted the occurrence of plant species with high biodiversity relevance, i.e., species that provide support for many other organisms (Table 1, Tyler et al., 2021). Thus, the relationship between rooting and downstream impacts on biodiversity is difficult to disentangle. This is probably confoundingly influenced by local conditions and abiotic factors like light, microclimate, species pool, and forest management. There is limited knowledge regarding ecosystem recovery following the removal or eradication of wild boar, making it difficult to predict long-term effects on plant communities or across different study systems. This warrants future research, especially as wild boar populations grow in size and distribution.

Wild boar rooting can enhance plant diversity in a boreal managed forest ecosystem, supporting broader conservation objectives such as the EU Biodiversity Strategy for 2030. In the present study area, wild boar are in the process re-establishing, which means their densities are relatively low, compared to other places throughout their established range (e.g., Pittiglio et al., 2018). The way wild boar use habitats and resources can be density-dependent (e.g., Augustsson et al., 2024), thus, while we can infer positive impacts of rooting on vascular plant communities, this might differ in areas with higher wild boar densities, and warrants investigation. Rooting at high boar densities in other contexts

may compromise forest regeneration, soil stability, and perhaps even invasive species control (Singer et al., 1984; Tierney and Cushman, 2006; Siemann et al., 2009; Spear and Chown, 2009; Barrios-Garcia and Ballari, 2012; Barrios-Garcia et al., 2023). This also underscores the need for adaptive management that balances biodiversity benefits with potential risks. Practical measures could include regulating population densities through hunting, monitoring rooting intensity as an ecological indicator, and integrating biodiversity goals into game and forest management plans. Recognizing wild boar as both a disturbance agent and a biodiversity facilitator may help reconcile wildlife management with conservation policy targets.

We found no support of maximized species diversity at intermediate levels of disturbance, as predicted with the IDH. Rather, we found a positive monotonic diversity-disturbance relationship (Fig. 2). According to the IDH, we expected diversity to decrease at higher levels of disturbance, due to the dominance of disturbance-adapted pioneer species. Although our result followed the expected trends of disturbance-dependent species being more common and competitive species being less common in more disturbed environments, it is possible that the process was restricted by the limited spatial and temporal scales of the experiment. A non-linear response to disturbance may also be masked by our use of broad disturbance categories. As the highest level of rooting intensity includes proportions of disturbed ground in the plot ranging from 51 to 100 %, it is likely that both conditions which promote diversity (i.e., moderate disturbance) and those that cause its decline (i.e., high disturbance) are present within the same category. Furthermore, as diversity may depend on a combination of different aspects of disturbance, such as intensity and frequency, (Hall et al., 2012), adding estimates of disturbance frequency over time may also improve. Finally, as discussed, wild boar densities are an important confounding factor to the impact that rooting has on the ecosystem, and in our system the densities of wild boar are relatively low. In our study, it was not possible to grade disturbance at a finer scale, nor could we control the intensity and frequency of disturbance, or account for changing/higher wild boar densities, however future studies should endeavour to do so (e.g., through exclusion experiments) to improve understanding of these relationships.

Finally, we found a strong effect of the local environmental context, i.e., the surrounding forest. In our study, the effects of rooting were pronounced in young forests and in areas with a high proportion of deciduous tree species. This suggests that disturbance events/pulses are not all equal, even at a fine-spatial scale as in our study. Instead disturbances are part of a dynamic process, and singularly isolating intensity or frequency mechanisms may not always be possible or realistic in the real world, nor the correct mechanism driving changes in local diversity (Sheil and Burslem, 2013; Jentsch and White, 2019). Instead mechanistic explorations must expand to include the interacting factors of local environment and disturbance together, to account for changes in resource and energy flows through the ecosystem (Jentsch and White, 2019). Further quantification in dynamic responses to disturbance may provide insights into these relationships and further disturbance ecology as a discipline.

5. Conclusion

Managed boreal forests often experience few natural disturbances and can become ecologically homogenized due to practices that promote uniform successional stages, and short harvest-rotation times. In such landscapes, physical disturbance by wild boar can enhance the richness and diversity of vascular plant species. We found that wild boar rooting had an overall positive effect on local vascular plant species richness and species diversity. Furthermore, rooting can also affect the occurrence and distribution of specific plant traits, such as seed bank longevity, nectar production, and biodiversity relevance. By impacting different plants unevenly and shifting the competitive advantage among species with certain ecological traits, wild boar rooting also has the potential to

alter local plant community composition, which in turn can contribute to broader ecological shifts. Given that such severe changes in plant composition can influence ecosystem function and services, we recommend further studies focused on long-term, large-scale plant dynamics. These studies should ideally include examinations of plant-insect interactions to facilitate a more comprehensive understanding of how these processes unfold across trophic levels and the lasting effects of wild boar disturbance on overall biodiversity. Moreover, our research highlights that local conditions are vital when assessing the effects of disturbance on plant diversity. The ecological impacts are interdependent on the extent of disturbance and the specific conditions of the ecosystem in which it occurs. Lastly, as several ungulate species experience rapid range expansion and population growths, alongside increased local animal traffic and aggregation due to supplementary food sources, we face potentially significant impacts on habitat and biodiversity. Therefore, changes in management practices, such as feeding regimes, could alter how ungulates affect plant communities and ecosystem processes.

CRediT authorship contribution statement

Evelina Augustsson: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Petter Kjellander:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Henrik Andrén:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Erik Öckinger:** Writing – review & editing, Methodology, Investigation. **Manisha Bhardwaj:** Writing – review & editing, Supervision, Methodology, Formal analysis.

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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. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.127552>.

Data availability

doi: 10.6084/m9.figshare.28919402 has been reserved for data and code, which will be made available upon acceptance of the manuscript

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