Long-term responses of boreal forest understory communities to sewage-sludge-derived and mineral fertilization in northern Sweden

Joachim Zutter

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Swedish University of Agricultural Sciences, SLU
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Långsiktiga effekter av avloppsslambaserad gödsling och konventionell mineralgödsling på markvegetationen i boreala skogar i norra Sverige

Joachim Zutter

Supervisor:	**Maja Sundqvist, SLU, Department of Forest Ecology and Management**
Assistant supervisor:	Johan Lundbäck, Sveaskog, SLU, Department of Forest Ecology and Management
Examiner:	Marie Charlotte Nilsson Hegethorn, SLU, Department of Forest Ecology and Management

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Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Forest Ecology and Management

Abstract

Forest fertilization can increase tree growth in nutrient-limited boreal forests, yet its influence on understory vegetation may remain detectable over the long term. This study examined the effects of conventional mineral fertilization and organic fertilization using pelletized and granulated wastewater-derived sludge on understory vegetation in northern Sweden 18–20 years after the initial treatment. Thirteen sites in Norrbotten county were investigated. Each site contained mineral-fertilized, biofertilized and unfertilized control areas, with 25 vegetation plots surveyed per treatment and 975 plots in total. Vascular plant, bryophyte taxa and their respective cover were measured within each plot, as well as the lichen cover. The analyses examined species richness at plot and treatment-area scales, within-area beta diversity, community composition, functional-group and species-level cover and occurrence. Community-weighted ecological indicator values for nitrogen, phosphorus and light were also assessed, alongside relationships between species richness and environmental covariates.

Long-term differences in the understory vegetation were detected between all three treatments. Species richness was higher in fertilized stands, and treatment significantly affected community composition. Within-area beta diversity did not differ significantly among treatments for either Bray–Curtis or Jaccard dissimilarities. Fertilization increased forb and graminoid cover and reduced dwarf-shrub cover. Several nutrient-associated species, including *Avenella flexuosa* (wavy hair-grass), increased following biofertilization, whereas *Vaccinium vitis-idaea* (lingonberry) declined. Community-weighted ecological indicator values indicated a shift toward species associated with more mesotrophic and lower-light conditions. Ground lichen cover was lower under both fertilization treatments, while occurrence was lower only in biofertilized stands. Finally, fertilization remained a significant predictor of richness and community composition after accounting for other environmental covariates, explaining 8.1% of Bray–Curtis and 5.5% of Jaccard variation.

Higher species richness therefore coincided with altered community composition and declined in characteristic components of nutrient-poor boreal forest floors, such as dwarf shrubs and ground lichens. Several responses were strongest under biofertilization, although the two fertilizer treatments differed in nutrient composition and total nitrogen input. These findings provide new evidence on the long-term effects of forest fertilization and contribute knowledge on the potential use of organic fertilizers as an alternative to large-scale mineral fertilization.

Keywords: boreal forest, forest fertilization, understory vegetation, biofertilization, species richness, community composition, functional groups, ground lichens

Sammanfattning

Skogsgödsling används för att öka trädens tillväxt i näringsbegränsade boreala skogar, men kan även orsaka långvariga förändringar i markvegetationens artsammansättning och mångfald. Denna studie undersökte effekterna av konventionell mineralgödsling och organisk gödsling med avloppsslam som torkats och bearbetats till pellets eller granulat på markvegetationen i norra Sverige 18–20 år efter den ursprungliga behandlingen. Tretton bestånd i Norrbottens län undersöktes. Varje lokal omfattade mineralgödslade, organiskt gödslade och ogödslade kontrollytor, med 25 vegetationsytor inventerade per behandling och totalt 975 provytor. Kärlväxt- och mossarter samt deras respektive täckningsgrad registrerades i varje provyta, liksom marklavarnas täckningsgrad. Analyserna omfattade artrikedom på provyte- och behandlingsområdesnivå, betadiversitet inom behandlingsområden, artsammansättning samt funktionella gruppers och enskilda arters täckningsgrad och förekomst. Samhällsviktade ekologiska indikatorvärden för kväve, fosfor och ljus analyserades också, liksom sambanden mellan artrikedom och miljövariabler.

Långvariga skillnader i markvegetationen påvisades mellan behandlingarna. Artrikedomen var högre i gödslade bestånd, och behandling hade en signifikant effekt på samhällssammansättningen. Betadiversiteten skilde sig inte signifikant mellan behandlingarna, vare sig med Bray–Curtis eller Jaccards olikhetsmått. Gödsling ökade täckningen av örter och gräs och minskade täckningen av risväxter. Flera näringsgynnade arter, som *Avenella flexuosa* (kruståtel), ökade efter biogödsling, medan *Vaccinium vitis-idaea* (lingon) minskade. Ekologiska indikatorvärden visade en förskjutning mot arter associerade med mer mesotrofa och ljusfattigare förhållanden. Marklavarnas täckning var lägre i båda gödslingsbehandlingarna medan förekomsten endast var lägre i biogödslade bestånd. Slutligen förblev gödsling en signifikant förklarande faktor för både artrikedom och samhällssammansättning efter att andra miljövariabler hade beaktats, och förklarade 8,1% av variationen i Bray–Curtis och 5,5% av variationen i Jaccard.

Den högre artrikedomen sammanföll därmed med förändrad samhällssammansättning och minskningar av karaktäristiska komponenter i näringsfattiga boreala skogsmarker, såsom risväxter och marklavar. Flera responser var starkast efter biogödsling, även om de två gödslingsbehandlingarna skilde sig åt i näringssammansättning och total kvävetillförsel. Resultaten bidrar med ny kunskap om gödslingens långsiktiga effekter på markvegetationen och ger även

kunskap om användningen av organiska gödselmedel, vilket betraktas som ett möjligt alternativ till storskalig användning av mineralgödsel.

Nyckelord: boreal skog, skogsgödsling, markvegetation, biogödsling, artrikedom, artsammansättning, funktionella grupper, marklavar

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which included site, treatment area within site, and transect within treatment area as random effects. Main effects were tested using Type II Wald F-tests with Kenward–Roger adjustment. The stand age × treatment interaction was significant (BH-adjusted p = 0.014), although the main effect of stand age was not. For community composition, bars show marginal PERMANOVA R^2 from models including treatment and all environmental covariates simultaneously, based on Bray–Curtis dissimilarities of square-root-transformed mean species cover and Jaccard dissimilarities of presence–absence data. PERMANOVA tests used 9,999 permutations with permutation structure matched to the spatial level of each predictor. Blue bars indicate significant effects; grey bars indicate non-significant effects. 34

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Abbreviations

Abbreviation	Description
ANOVA	Analysis of variance
CWM	Community-weighted mean
FDR	False discovery rate
GPS	Global Positioning System
LMM	Linear mixed-effects model
NMDS	Non-metric multidimensional scaling
NPP	Net primary production
PERMANOVA	Permutational multivariate analysis of variance
PERMDISP	Permutational analysis of multivariate dispersions
SLU	Swedish University of Agricultural Sciences
SP.	One unspecified species within a genus, e.g. *Pinus* sp.
SPP.	Multiple species within a genus, e.g. *Pinus* spp.
SYVAB	Sydvästra Stockholmsregionens VA-verksaktiebolag
UMEVA	Umeå Vatten och Avfall AB
WGS 1984	World Geodetic System 1984

1. Introduction

The boreal forest is the largest terrestrial biome on Earth, extending across North America, Russia and Fennoscandia. Boreal forests store a large proportion of global soil carbon, with more than half of their total ecosystem carbon stocks stored belowground (Stendahl et al. 2010; Bradshaw & Warkentin 2015). Tree growth in boreal forests is mainly limited by low nitrogen availability (Tamm 1991; LeBauer & Treseder 2008).

Swedish forestry is strongly shaped by rotational forestry, practised in 96% of Swedish managed forests, where clearcutting is commonly used as the harvesting method, often followed by soil preparation and assisted regeneration (Axelsson & Angelstam 2011). In Swedish commercial forestry, nitrogen fertilization stimulates stem growth, increase timber yield and increased short-term carbon uptake (Boeraeve et al. 2025).

Rising atmospheric CO_2 levels are now resulting in progressive nitrogen limitation in Sweden's boreal forests (Bassett et al. 2026). In the context of global warming, interest in forest fertilization has increased as a potential climate-change mitigation tool (Jämtgård et al. 2026). Fertilization can increase tree biomass and carbon storage in boreal forests (Jorgensen et al. 2021), although these benefits do not necessarily extend to soil carbon, which may decline under altered decomposition and microbial processes (Jorgensen et al. 2021; Blaško et al. 2022).

Nitrogen fertilization can also alter soil fungal communities, including ectomycorrhizal fungi, which play important roles in nutrient cycling and soil carbon dynamics (Högberg et al. 2014; Jörgensen et al. 2022). Beyond its effects on soil processes, fertilization can also generate trade-offs for other ecosystem services, particularly biodiversity. In northern Fennoscandia, such impacts may also have socioecological implications for Sámi reindeer husbandry, as reindeer (*Rangifer tarandus tarandus*) depend on lichens during winter and fertilization can reduce ground lichen abundance (Olsson & Kellner 2006; Kivinen et al. 2010).

Understory vegetation is a central component of boreal forest ecosystems that contributes to nutrient cycling, carbon dynamics and habitat provision. Dwarf shrubs and particularly *Vaccinium* species, which often dominate the boreal forest floor (Andersson 2021), have important effects on nutrient dynamics and food webs (Hedwall 2012). Across boreal forests, nitrogen fertilization, together with natural deposition, have altered the composition of understory vegetation, with responses varying considerably among functional groups, sites and fertilization regimes (Sullivan & Sullivan 2018). In Fennoscandian boreal forests, increased nitrogen availability has been associated with shifts from slow-growing, nutrient-conservative species towards a more nutrient-demanding vegetation. Nitrogen addition in northern Finland led to a reduction of biomass for *Vaccinium myrtillus* (bilberry) while increasing *Avenella flexuosa* (wavy hair-grass) and other

graminoids (Manninen et al. 2009). Similarly, repeated commercial fertilization in Sweden has been associated with declines in dwarf shrubs, increases in grasses and herbs, reduced berry production and annual shoot growth for *V. myrtillus* (Strengbom & Nordin 2008).

Non-vascular vegetation can also be altered by fertilization. A reduction in cover and species richness for bryophytes and ground-lichens was still detectable 15-18 years after the last nitrogen application in a Swedish boreal forest study (Olsson & Kellner 2006). Other Swedish experiments have demonstrated slow understory recovery after nitrogen addition (Strengbom et al. 2001), although communities may converge several decades later (Larsson et al. 2024). These experiments also show that understory responses depend not solely on nutrient addition itself, but also on fertilizer dose, composition, frequency and time since application (Olsson & Kellner 2006; Strengbom & Nordin 2008; Larsson et al. 2024).

Research on understory responses has primarily focused on mineral nitrogen fertilizers, while organic alternatives remain less studied. Such organic fertilizers may differ substantially from conventional fertilizers in their nutrient composition, total application rates and temporal nutrient availability. For example, sewage-sludge application in Swedish Scots pine (*Pinus sylvestris*) dominated forests increased soil concentration of several nutrients, including N, P, K, Ca and Mg, with some effects remaining detectable over a decade after application (Bramryd 2002). Consequently, organic fertilizers could potentially produce vegetation responses that differ in magnitude and/or persistence from those caused by mineral fertilizers, but their long-term effects on understory diversity and community composition are poorly understood.

Long-term boreal forest monitoring has demonstrated that understory vegetation responds to interacting effects of nitrogen availability, forest density, climate and soil conditions (Hedwall et al. 2021). Understory composition is strongly associated with overstory canopy cover and leaf area index (Majasalmi & Rautiainen 2020). Soil moisture, site fertility and tree-species composition can further influence resource availability and competitive relationships among understory species. Evaluating both fertilization treatment and environmental variation can therefore help distinguish treatment-related changes from differences associated with local site conditions.

This study aims to assess the long-term effects of mineral and organic fertilization on understory vegetation composition, diversity and functional groups in boreal Sweden, compared with unfertilized controls, while accounting for environmental variation and potential interactions with fertilization. To achieve this, I used a study system originally established by Sahlén (2012) ~20 years ago to evaluate the effects of fertilization on timber growth and carbon sequestration. The treatments consist of conventional mineral fertilization and fertilization with Bionäring, a pelletized sewage-sludge-derived product (hereafter referred to as

organic fertilization). Compared with conventional mineral fertilizers, the organic fertilizer is expected to release nutrients more gradually (Sahlén et al. 2011; Sahlén 2012; Näslund 2015).

Given that I surveyed vegetation 18–20 years after the initial applications considering fertilization as the only forest management method, this study adds to existing long-term evidence, particularly regarding the less-studied effects of organic fertilization. In order to assess potential ecological shifts, I used ecological indicator values for Swedish vascular plants (Tyler et al. 2021). These values were cover-weighted to the data that I collected within each community to characterize associations for each treatment with nitrogen, phosphorus and shade tolerance. I did not find any corresponding study for bryophytes which are therefore not included. To better understand the effects of forest fertilization on understory vegetation and contribute to more sustainable forest management, this study addresses the following research questions and hypotheses:

(i) How do mineral and organic fertilization differ in their long-term effects on understory species richness, community composition, functional groups and individual species?
(ii) Do the fertilization treatments lead to a shift in ecological characteristics of understory vegetation communities for nitrogen, phosphorus and light?
(iii) How important is fertilization relative to other the local environmental variation in explaining understory species richness and community composition, and does the local environment affect understory response to fertilization?

H1: Based on previously reported long-term responses of understory vegetation to nutrient addition, both fertilization treatments are expected to reduce species richness and the cover of dwarf shrubs, bryophytes and lichens, while increasing forb and graminoid cover (Olsson & Kellner 2006; Strengbom & Nordin 2008; Sullivan & Sullivan 2018). These effects are expected to be stronger under biofertilization than mineral fertilization due to its higher nutrient input and more gradual nutrient release.
H2: Fertilization is expected to favour understory species associated with higher nutrient availability. Fertilization may also stimulate vegetation growth, increasing shading and favouring species associated with lower light availability. Under both fertilization treatments, understory communities are therefore expected to have higher community-weighted indicator values for nitrogen and phosphorus and lower for light than in unfertilized controls.
H3: Fertilization treatment is expected to explain a larger proportion of the variation in understory species richness than any individual environmental covariate and to retain a significant effect after accounting for stand age, soil moisture, altitude, latitude, distance to open environment and dominant tree group.

2. Methodology

2.1 Study area

This study covered 13 stands owned by Sveaskog across the municipalities of Kalix, Överkalix and Övertorneå in the county of Norrbotten, Sweden (Figure 1).

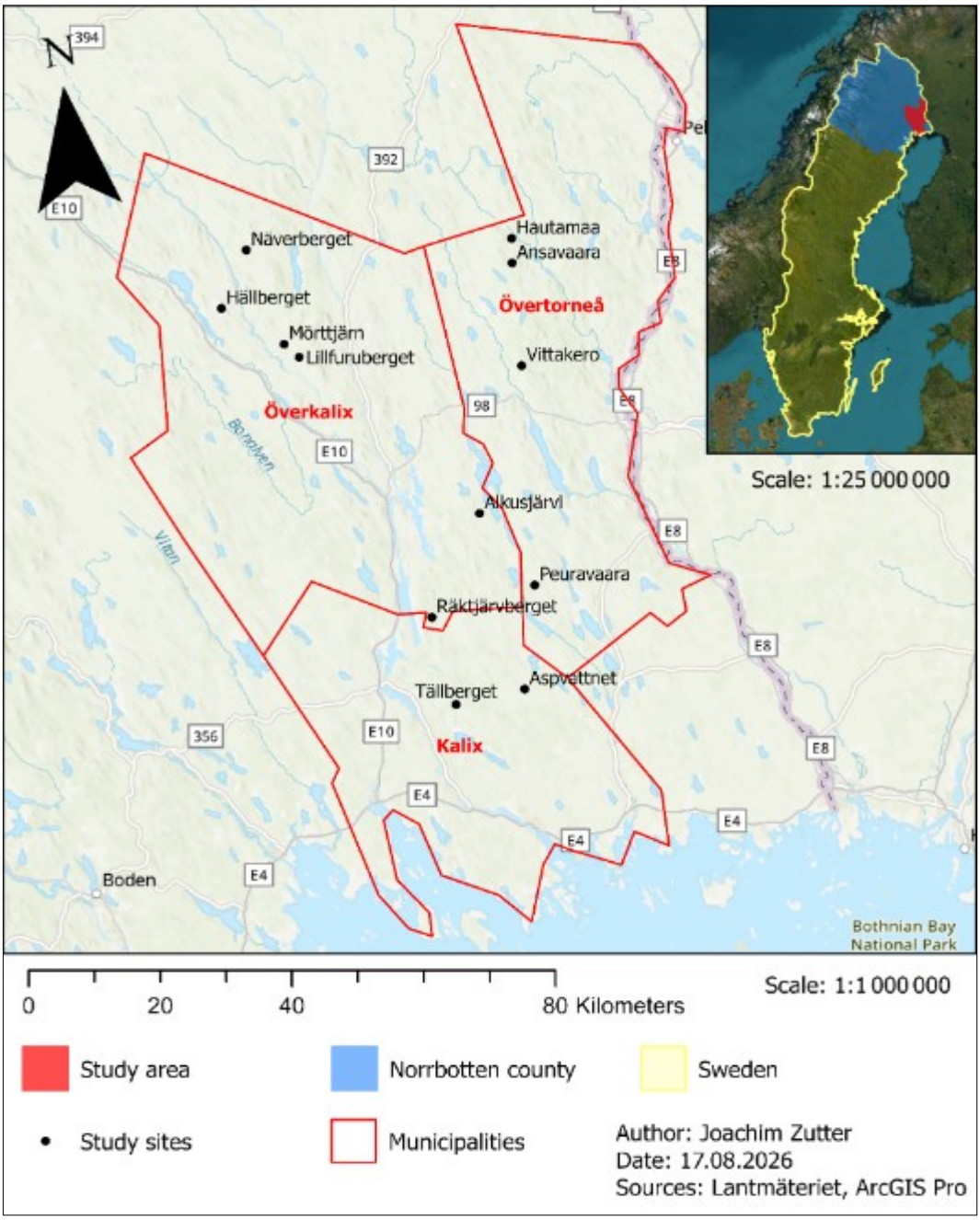


Figure 1: Location and distribution of the 13 forest stands surveyed in this study across the municipalities of Kalix, Överkalix and Övertorneå in Norrbotten County, northern Sweden.

2.2 Environmental context

The climate in this region of Norrbotten is classified as subarctic (dfc according to Köppen-Geiger classification (Rydén 2025)). Lingonberry (*Vaccinium vitis-idaea*) and bilberry (*Vaccinium myrtillus*) are frequently the dominant understory species in this eastern part of Norrbotten, while grass species may dominate at smaller scales on fertile soils (Andersson 2021). The most common tree species across the sites were Scots pine, Norway spruce (*Picea abies*) and birches (*Betula pendula* & *B. pubescens*) (Sahlén 2012). The sites were situated between 66 and 67° N and at altitudes ranging from 83 to 246 m a.s.l (mean = 149 m a.s.l; Table 1). According to Sahlén (2012), the most widespread understory vegetation type and species consisted of lingonberry, while herbs, grasses and bilberries were locally dominant. Site productivity was classified as 18-22 for Scots pine and 16-18 for Norway spruce (Sahlén 2012), meaning that after 100 years of forest growth the dominant Scots pines in the stand should be able to reach 18-22 m in height, respectively 16-18 m in height for Norway spruce (Andersson et al. 2021). The stand ages across the surveyed forests ranged from 39 to 97 years (mean = 64) (Sahlén 2012).

Table 1: Environmental characteristics of the 13 study sites, including altitude (m), understory vegetation type according to Sahlén (2012), growth index, stand age at initial fertilization, and stand age adjusted to 2026 (Sahlén, 2012).

Site	Altitude (m)	Understory vegetation type*	Growth index**	Stand age at initial fertilization	Adjusted stand age (2026)
Näverberget	245	L	P20	64	84
Mörttjärn	83	L	P18	77	97
Hällberget	246	L	P19	19	39
Lillfuruberget	95	L	P20	55	75
Tällberget 6	101	G	P22	32	51
Ansavaara	220	Lh/G	S17	40	59
Peuravaara	115	B/Lh	P18	37	56
Alkusjärvi	151	L	P19	42	60
Hautamaa	200	G	S18	31	49
Vittakero	185	Lh	S16	45	63
Räktjärvberget 36/37	85	B/L	P20	43	61
Räktjärvberget 39	101	B/L	P19	41	59
Aspvattnet	106	B/L	P19	50	69

Abbreviations referring to: *L = Lingonberry, Lh = Low herb, G = Grass, B = Bilberry ; **P = Pine, S = Spruce.

2.3 Fertilization context

The description of the original fertilization experiment presented below is based on Sahlén (2012). Each forest stand was divided into separate areas receiving one of three treatments: 1) unfertilized control, 2) mineral fertilization using SkogCan (hereafter referred to as mineral), and 3) organic fertilization using the sewage-sludge-derived product Bionäring (hereafter referred to as bio). Treatment areas were delineated to be as similar as possible in tree species composition, basal area, stand age and site productivity (Sahlén 2012). SkogCan is produced by the company Yara AB (Malmö, Sweden) and mainly consists of ammonium nitrate (NH_4NO_3) as a nitrogen source. It contains ~27% of total nitrogen, 13.5% of ammonium nitrogen, 20% of dolomite limestone, which leads to high concentrations of calcium and magnesium. The organic fertilizer originates from municipal wastewater treatment plants from southern Stockholm (SYVAB) and Umeå (UMEVA). The sludge originating from wastewater undergoes anaerobic digestion to produce biogas and the remaining digestate is dried and pelletized or granulated (Sahlén 2012). These organic fertilizers contain 3–4 % of nitrogen, ~3% of phosphorus and about two-thirds of the dry mass consists of organic matter (Sahlén 2012). Most of the nitrogen in Bionäring is organically bound and becomes available to plants progressively through mineralization, unlike the more readily available inorganic nitrogen in conventional mineral fertilizers (Sahlén et al. 2011; Näslund 2015). The application rate for the organic fertilizer ranged between 358 and 694 kg N/ha (mean = 532 kg N/ha), applied once (2006-2008). Mineral fertilizer was applied at lower nitrogen application rates, ranging from 101 to 176 kg N/ha (mean = 142 kg N/ha) in 2006-2008, followed by a second application with a standard dose of 150 kg N/ha of SkogCan on all mineral-fertilized sites three years after the initial application (2009-2011). The total nitrogen addition was thereby almost twice as high in biofertilized stands for practical reasons compared to mineral fertilized stands, even after the second application.

2.4 Study protocol

The coordinates of each plot (XY, GCS WGS 1984) were calculated in ArcGIS Pro 3.6 and used as a reference to find the plots during fieldwork. Five transects (100 m each) were established within an area of 2.5–3.5 ha along a north-south axis within each of the treatments at each of the 13 sites. Along each transect, five sampling plots were positioned at 25 m intervals, resulting in 25 plots/treatment, 75 plots/site and 975 plots in total across the 13 sites (Figure 2). To cover similar sampling distances across all treatments, transects were spaced ~50 m apart where stand geometry and treatment size permitted. However, given that the pre-established stands and respective treatments areas (Sahlén 2012) had variable areas,

transect spacing was adjusted where necessary while maintaining comparable sampled areas among treatments. In that case, the positions of the transects were adjusted to fit a similar sampling surface across all treatments of the stand. Furthermore, the transects were positioned at a minimum distance of 25 m from the treatment boundary, to limit edge effects. All maps used as references during the fieldwork are available in the Appendices (Appendix 1 to 12).

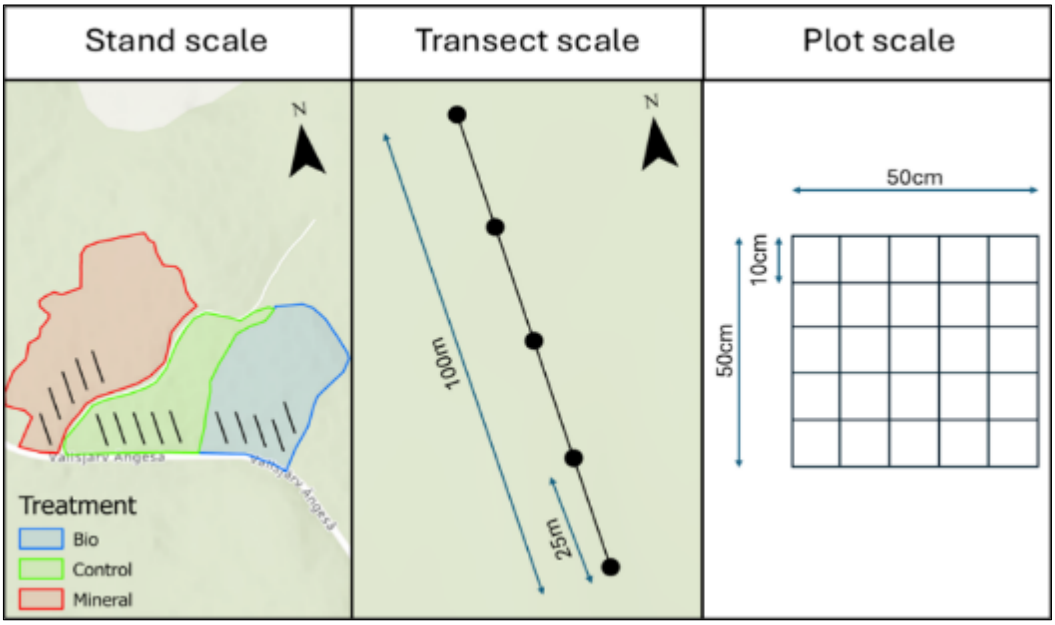


Figure 2: Schematic representation of the sampling design at stand, transect and plot scales. Each forest stand contained three treatment areas (biofertilized, mineral-fertilized and control), each sampled using five 100-m transects. Five vegetation plots were positioned at 25-m intervals along each transect, resulting in 25 plots per treatment area and 75 plots per stand. Each plot measured 50 × 50 cm, as illustrated by the 10 × 10 cm grid in the right panel.

Before field measurements, the following environmental variables were recorded for each plot and subsequently used as covariates in the analyses to better understand the effects of fertilization on species richness and community composition: treatment type (Bio, Mineral, Control), altitude (m a.s.l) (Sahlén 2012), latitude (°N), distance to the nearest open habitat or structure (m, road wider than 2 m, open mire or recent clearcut), current stand age, stand age at the time of initial fertilization (Sahlén 2012) and soil moisture. Soil moisture conditions for each plot were derived from the SLU soil moisture map (sksSLUmfMarkfuktighet25) using ArcGIS Pro 3.6. Raster statistics were calculated using the "Calculate Statistics" geoprocessing tool, after which raster values were reclassified using the tool "Reclass by Table" into four ordinal soil moisture classes: dry, mesic-dry, mesic-moist, and moist. For each plot, the dominant soil-moisture class within a 3-m radius of the plot centre was assigned as the plot-level soil-moisture category (Appendix 13).

2.5 Field measurements

Fieldwork was conducted from 6th to 25th of July 2026. During fieldwork the dominant tree species based on basal area was noted in each of the five plots within each of the five transects in each treatment using a factor gauge. In these same plots within transects, understory vegetation was also assessed using a 50 cm × 50 cm quadrat subdivided into a 10 × 10 cm grid (Shin et al. 2014), by recording species and their cover (%) for all vascular plants, bryophytes and lycophytes within the 50 × 50 cm grid (Appendix 14). I used this data to calculate species richness, community structure, functional group cover and occurrence per 0.25 m^2 and conduct species level analyses. To assess species richness at site scale, additional species encountered outside the plots were also reported. To ensure equal sampling effort, these additional species were recorded only from the moment the first plot (within a treatment area) was sampled, until the 25th plot was completed. Ground lichen cover and presence/absence were recorded in all 975 plots using the same grid (0.25 m^2). These data were used to determine the effects of fertilization on lichen cover and occurrence separately from the other functional groups, given that lichens were not identified at the species level. Understory vegetation was defined as all non-woody taxa as well as woody taxa that do not grow taller than 2 m, hence excluding tree seedlings and saplings.

2.6 Statistical analyses

Statistical analyses were performed in R version 4.5.2, with statistical significance defined as $p < 0.05$. The study followed a blocked and hierarchical sampling design including 13 sites, each containing three treatment areas (mineral fertilization, biofertilization and control). Within each treatment area 25 plots (50 × 50 cm) were distributed along five transects. Because plots within the same treatment area were subsamples rather than independent treatment replicates, the sampling hierarchy was accounted for in the statistical analyses.

Analyses were conducted at either plot scale (n = 975) or treatment-area scale (n= 39), depending on the response variable. Plot-scale responses were analysed using linear mixed models (LMMs), fitted with the lme4 package (Bates et al. 2026). Treatment was included as a fixed effect, with random intercepts for site, treatment area, nested within site, and transect nested within treatment area. This structure accounted for the variation among sites and dependence among plots belonging to the same treatment area or transect. Treatment-area responses were analysed using either LMMs with site as a random intercept or blocked analysis of variance (ANOVA) with site as a fixed blocking factor. Both approaches accounted for the three treatments occurring within each site, although they differed in how site-level variation was represented.

The choice of statistical test depended on the response variable and model assumptions. Parametric model assumptions were evaluated using Q-Q plots, Shapiro tests for normality (Shapiro & Wilk 1965), and assessments of homogeneity of variance. When assumptions for blocked ANOVA were not adequately satisfied, Friedman tests (Friedman 1937) were used to compare treatment responses within sites without assuming normally distributed residuals. Significant treatment effects in parametric models were followed by pairwise comparisons of estimated marginal means using emmeans (Lenth et al. 2026). Following significant Friedman tests, pairwise comparisons were performed using paired Wilcoxon signed-rank tests (Wilcoxon 1945). Holm adjustment was applied to the three pairwise treatment comparisons within each response.

Two approaches were used to correct multiple comparisons. Holm adjustment (Holm 1979) was applied to post-hoc comparisons among the three treatments (Mineral-Control, Bio-Control and Bio-Mineral), controlling the family-wise error rate within each set of comparisons. Benjamini-Hochberg false discovery rate (BH-FDR) correction (Benjamini & Hochberg 1995) was used for families of simultaneous tests across multiple species or environmental predictors.

Community composition was analysed using Bray-Curtis dissimilarity (Bray & Curtis 1957), calculated from square-root-transformed species cover, and Jaccard dissimilarity (Jaccard 1908), calculated from presence-absence data. Treatment effects on community composition were assessed using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001), implemented with adonis2 in the vegan package (Oksanen et al. 2026).

2.6.1 Sampling completeness

Sampling completeness was assessed using randomized species accumulation curves and incidence-based Chao2 richness estimators (Chao 1987). Species presence-absence data were aggregated across the 25 (50 × 50 cm) plots within each treatment area, using the 13 sites as sampling units for each treatment. Accumulation curves were calculated using specaccum() in the vegan package, with 9,999 permutations. Chao2 richness was estimated using specpool() with small-sample correction. Sampling completeness was expressed as the percentage of estimated richness represented by observed species. The numbers of species occurring in only one or two sites were also examined to assess the influence of infrequent species on richness estimates.

2.6.2 Species richness response to fertilization

Species richness was analysed at two spatial scales to distinguish local richness from richness accumulated across treatment areas. Plot-scale alpha richness was defined as the number of species recorded within each 50 × 50 cm vegetation plot

(n = 975). Treatment effects were assessed using a nested linear mixed-effects model (LMM), with treatment as a fixed effect and random intercepts for site, treatment area within site and transect within treatment area. Treatment-area richness was defined as the total number of distinct species recorded within each treatment area (n = 39), including species from the supplementary inventory described in the field methods. At this scale, an LMM was fitted with treatment as a fixed effect and site as a random intercept.

For both models, overall treatment effects were tested using F-tests with Satterthwaite degrees of freedom, followed by Holm-adjusted pairwise comparisons of estimated marginal means. Model assumptions were evaluated using residual Q–Q plots, residual-versus-fitted plots and checks of homogeneity of variance.

2.6.3 Community structure response to fertilization

Within-area beta diversity was quantified as compositional heterogeneity among the 25 vegetation plots within each treatment area. For each treatment area (n = 39), beta diversity was calculated as the mean distance of plots to their multivariate median using betadisper in the vegan package, with bias adjustment (Stier et al. 2013) and Lingoes correction (Lingoes 1971). Bray-Curtis and Jaccard dissimilarities were analysed separately to assess variation in species cover and presence-absence, respectively. Treatment effects were tested using Friedman tests with site as the blocking factor.

Community composition was analysed separately to determine whether treatments differed in species identity and relative cover. Mean species cover across the 25 (50 × 50 cm) plots was used to represent each treatment-area community (n = 39). Bray-Curtis and Jaccard dissimilarity matrices were analysed using PERMANOVA (adonis2) with 9,999 permutations restricted within sites, followed by Holm-adjusted pairwise comparisons. Homogeneity of multivariate dispersion was assessed using betadisper and restricted permutation tests (permutest), because differences in dispersion can influence PERMANOVA results. Community composition was visualized using two-dimensional scaling (NMDS) (Kruskal 1964), based on Bray-Curtis dissimilarity, with 95% group confidence ellipses.

2.6.4 Functional-group responses to fertilization

Functional-group responses were assessed using two measures: mean cover and occurrence. Species were assigned to six functional groups: bryophytes, dwarf-shrubs (height < 1 m), shrubs (height > 1 m), graminoids, forbs, ferns (including lycophytes). Ground lichens were included as a seventh functional group but analysed from separately recorded total lichen cover, as lichen species were not identified.

For each functional group, total cover was calculated within each vegetation plot summing the cover of its constituent species, except for ground lichens, for which directly recorded cover was used. Mean cover was calculated across the 25 plots within each treatment area, including plots where the group was absent (n = 39). Because species cover values were summed, total functional-group cover could exceed 100% where species overlapped. Occurrence was calculated as the percentage of plots containing at least one species belonging to the group, or any ground lichens in the case of lichens. Treatment effects on mean cover were assessed using blocked ANOVA for bryophytes, dwarf shrubs, graminoids and forbs. For shrubs, ferns and ground lichens, Friedman tests were used because of zero-inflated cover distributions. Occurrence was analysed using Friedman tests for all seven functional groups, with site as the blocking factor. For the ANOVA models, residual normality and variance homogeneity were assessed using Shapiro-Wilk and Fligner-Killeen tests (Fligner & Killeen 1976), respectively, together with graphical residual diagnostics. BH-FDR correction was applied separately to the seven overall treatment tests for cover and the seven tests for occurrence. Holm-adjusted pairwise comparisons were used to identify differences between treatments within each functional group. Only functional groups showing significant treatment effects were displayed in the corresponding figures, while all seven groups were included in the statistical analyses.

2.6.5 Species-level response to fertilization

Individual species responses were assessed using three measures: mean cover across all plots including absences, occurrences (percentage of plots occupied), and conditional cover (mean cover in occupied plots only). Each measure was calculated separately for each species within each treatment area (n = 39). Treatment effects were assessed using two-sided paired randomization tests based on within-site differences for three predefined contrasts: Bio-Control, Mineral-Control and Bio-Mineral. For contrasts with 13 valid site pairs, all 8,192 possible sign permutations were evaluated. For conditional cover, only sites where the species occurred in both compared treatment areas were included, and comparisons with fewer than two valid pairs were not tested. This approach preserved the site-blocked design without requiring normally distributed species response. Effect sizes were expressed as mean paired differences in % for all measures. BH-FDR correction was applied separately to the species tests within each response × treatment contrast.

2.6.6 Community-weighted ecological indicator values

To assess whether fertilization altered the ecological affinities of understory communities, community-weighted mean (CWM) indicator values for nitrogen,

phosphorus and light were calculated using the Swedish ecological indicator values of Tyler et al. (2021). Higher indicator values represent species associated with higher levels of the corresponding environmental factor. Only vascular plants were included, as similar indicator values were not found within the literature for bryophytes.

For each treatment area (n = 39), species indicator values were weighted by their mean cover across the 25 50 × 50 cm vegetation plots. CWM values were calculated as the sum of species cover multiplied by their indicator values, divided by the total cover of species with available indicator values. These values therefore describe the ecological affinities of the vegetation communities rather than directly measured environmental conditions. Treatment effects were assessed separately for nitrogen, phosphorus and light using blocked ANOVA, with site as the blocking factor, followed by Holm-adjusted pairwise comparisons. Model assumptions were evaluated using residual diagnostics and Shapiro-Wilk tests.

2.6.7 Environmental covariates

To understand the effect of environmental variation compared to fertilization and their influence on the understory's response to fertilization, seven covariates were included in the models including soil moisture, dominant tree group, stand age, years since fertilization, altitude, latitude and distance to open environment. These covariates were selected to represent variation in local habitat conditions, forest structure and geographical position, which may influence understory vegetation independently of fertilizer treatment. Continuous predictors were centred and scaled, and collinearity was assessed using correlations and variance inflation factors.

Plot-scale species richness (n = 975) was analysed using a LMM with treatment and all seven covariates as additive fixed effects. Random intercepts for site, treatment area nested within site and transect nested within treatment area accounted for the hierarchical sampling design. Main effects were assessed using Type II Wald F-tests (Kenward & Roger 1997). Marginal and conditional R^2 were calculated using the performance package (Lüdecke et al. 2026). The independent contribution of each predictor was quantified as the reduction in marginal R^2 when that predictor was removed from the full model, while retaining all other predictors. Community composition was analysed at the treatment-area scale (n = 39) using PERMANOVA on Bray-Curtis and Jaccard dissimilarities. Treatment and all seven covariates were included simultaneously, and marginal PERMANOVA R^2 quantified each predictor's contribution after accounting for the others. For community-composition analyses, plot-level soil moisture and distance to open environment were averaged within treatment areas. Dominant tree group was classified as *Pinus* or *Picea* when at least 70% of plots belonged to that group. All remaining areas, including broadleaf-dominated areas, were classified as mixed.

Significance was assessed using 9,999 permutations, restricted within sites for treatment-area predictors and applied to complete site blocks for predictors varying only between sites.

To assess whether environmental conditions modified the fertilization response of species richness, seven additional LMMs were fitted, each including one treatment × covariate interaction while retaining all main effects and the original random-effects structure. Interactions were evaluated using Type III Wald F-tests, with BH-FDR correction across the seven tests. The significant treatment × stand age interaction was further examined using treatment-specific slopes and Tukey-adjusted pairwise slope comparisons calculated with emmeans.

2.6.8 Synthesis of the statistical analyses

Statistical analyses were selected according to the response variable, sampling scale and experimental design. Table 2 provides an overview and summary of the approaches that were used throughout the study and their respective objectives.

Table 2: Overview of statistical methods used to assess long-term fertilization effects on understory vegetation, organized by response variable and sampling scale. Analyses were conducted at either plot scale (n = 975) or treatment-area scale (n = 39; three treatments paired within 13 sites). LMM = linear mixed model; PERMANOVA = permutational multivariate analysis of variance; NMDS = non-metric multidimensional scaling.

Response	Sampling scale	Statistical method
Sampling completeness	Treatment area (n = 39)	Species accumulation curves + Chao2 estimator
Species richness	Plot (n = 975)	Hierarchical LMM (site, treatment area and transect as random effects)
	Treatment area (n = 39)	LMM (Site as random intercept)
Community structure	Treatment area (n = 39)	Multivariate dispersion + Friedman tests + PERMANOVA (NMDS visualization)
Functional groups	Treatment area (n = 39)	Blocked ANOVA + Friedman tests
Individual species	Treatment area (n = 39)	Exact paired randomization tests
Ecological indicators	Treatment area (n = 39)	Blocked ANOVA
Environment covariates	Plot (n = 975)	Hierarchical LMM + Type II and Type III F-tests
	Treatment area (n = 39)	Covariate-adjusted PERMANOVA

3. Results

3.1 Sampling completeness

Species accumulation curves increased during the first sampled sites before gradually approaching an asymptote for all treatments (Figure 3). Biofertilized stands accumulated the highest number of species throughout the sampling sequence, reaching an observed richness of 71 species, compared with 64 species in mineral-fertilized stands and 60 species in control stands. By the tenth sampled site, the accumulation curves reached 93% of the final observed richness for biofertilized stands, and 94% for mineral-fertilized and control stands. Incidence-based Chao2 estimators suggested that additional species remained undetected within all treatments. Estimated total richness was 97 species for biofertilized stands, 76 for mineral stands and 75 for control stands. These estimates correspond to sampling completeness values of 72.9%, 84.2% and 80.2% respectively.

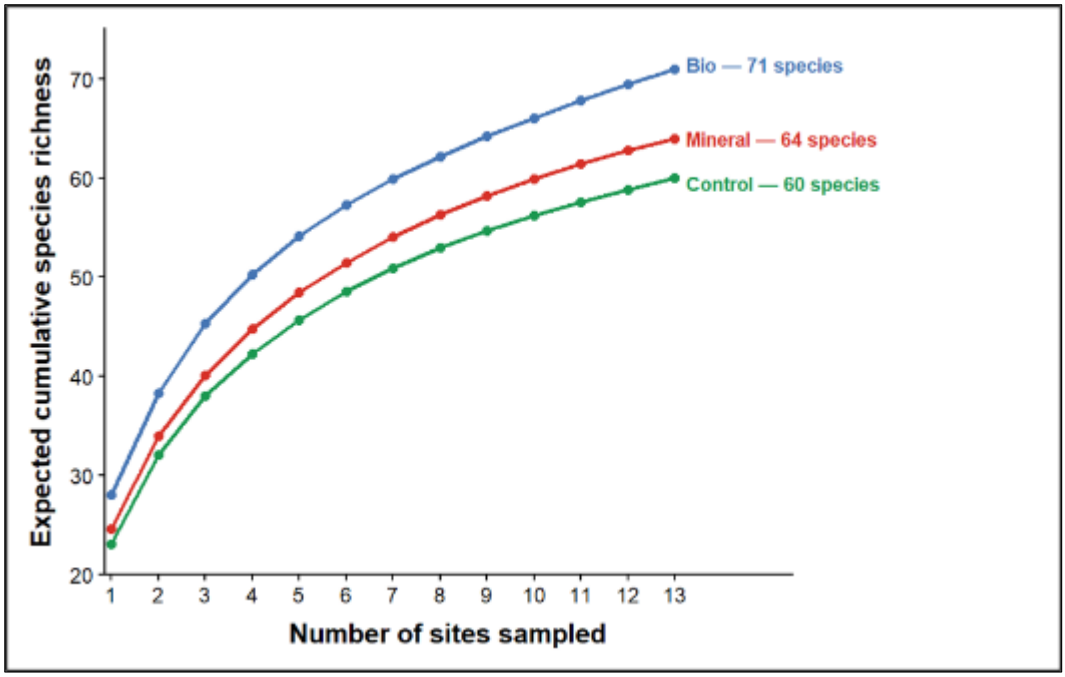


Figure 3: Randomized species accumulation curves showing mean cumulative understory species richness with increasing numbers of sampled sites for three long-term fertilization treatments in northern Swedish boreal forests (n = 13 sites per treatment). Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. Curves were generated using 9,999 randomizations of site order, and labels indicate observed richness across all 13 sites.

3.2 Species richness response to fertilization

A total of 104 species were recorded across the study sites, including 89 within vegetation plots. Species recorded during the supplementary inventory were included only in treatment-area richness calculations. Species richness differed significantly among fertilization treatments at both plot and treatment-area scales (Figure 4). At plot scale, the treatment effect was significant (LMM: $F_{2,24} = 26.00$, $p < 0.001$). Plot-scale species richness was highest under biofertilization (9.27 species per plot), followed by mineral fertilization (8.58) and control (7.33). Holm-adjusted pairwise comparisons showed significant differences between all treatments (Bio–Control: $p < 0.0001$; Bio–Mineral: $p = 0.019$; Mineral–Control: $p = 0.0002$). Treatment-area species richness showed the same pattern (LMM: $F_{2,24} = 14.68$, $p < 0.001$), with the highest mean under biofertilization (37.6 species per treatment area), followed by mineral fertilization (33.0) and control (29.5). All pairwise differences were significant after Holm adjustment (Bio–Control: $p < 0.0001$; Bio–Mineral: $p = 0.010$; Mineral–Control: $p = 0.030$). Model diagnostics showed no significant departure from residual normality for treatment-area richness (Shapiro–Wilk: $W = 0.981$, $p = 0.745$). Plot-scale richness showed a significant deviation ($W = 0.988$, $p < 0.001$), mainly in the distribution tails. Nevertheless, visual inspection of residual Q–Q, residual-versus-fitted and scale-location plots revealed no substantial patterns or pronounced heteroscedasticity.

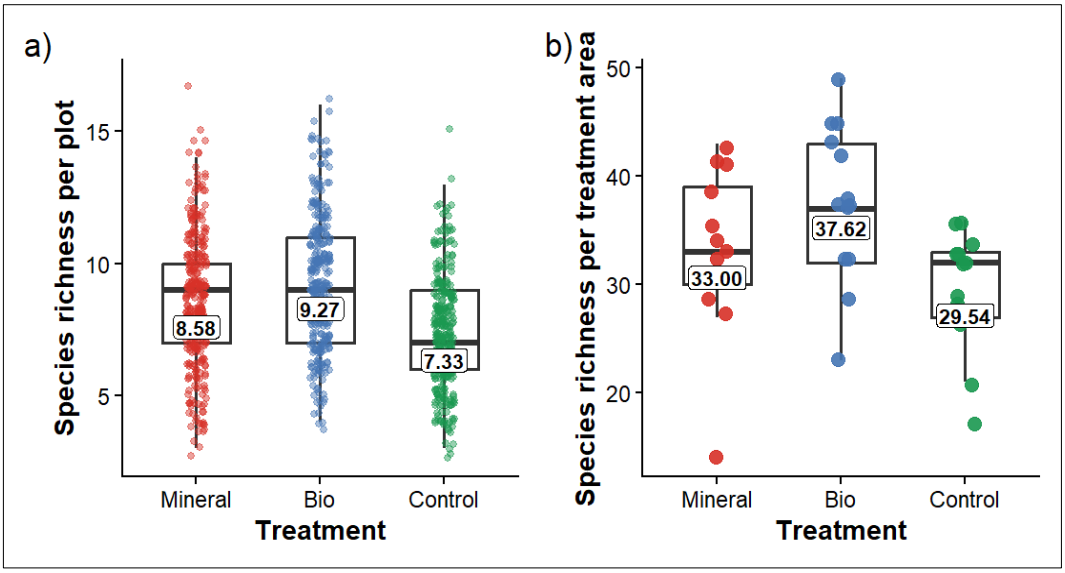


Figure 4: Effects of long-term forest fertilization on (a) species richness per plot (n = 325 per treatment) and (b) total species richness per treatment area (n = 13 per treatment) in northern Swedish boreal forests. Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. Points represent observations; boxes show the interquartile range (25th–75th percentiles), horizontal lines indicate medians, whiskers extend to 1.5 times the interquartile range, and numerical labels show means. Treatment effects were tested using hierarchical linear mixed-effects models with Holm-adjusted pairwise comparisons.

3.3 Community structure response to fertilization

Fertilization did not significantly affect within-treatment-area beta diversity. Mean Bray–Curtis beta diversity was 0.458 in mineral-fertilized areas, 0.442 in biofertilized areas and 0.457 in controls, with no significant treatment effect (Friedman $\chi^2_2 = 2.46$, $p = 0.292$). Similarly, mean Jaccard beta diversity was 0.473, 0.465 and 0.485, respectively, and did not differ significantly among treatments (Friedman $\chi^2_2 = 4.31$, $p = 0.116$).

Community composition differed significantly among treatments. Bray–Curtis PERMANOVA detected a treatment effect ($F_{2,36} = 1.81$, $R^2 = 0.092$, $p < 0.001$), with significant differences between Bio–Control ($R^2 = 0.113$, $p < 0.001$) and Mineral–Control ($R^2 = 0.065$, $p < 0.001$), but not Bio–Mineral ($p = 0.067$). Jaccard PERMANOVA also detected a treatment effect ($F_{2,36} = 1.10$, $R^2 = 0.057$, $p < 0.001$), although only Bio–Control differed significantly ($R^2 = 0.060$, $p < 0.001$). All pairwise p-values were Holm-adjusted. Multivariate dispersion did not differ significantly among treatments for Bray–Curtis ($p = 0.733$) or Jaccard ($p = 0.868$). NMDS showed substantial overlap among treatments (stress = 0.109; Figure 5).

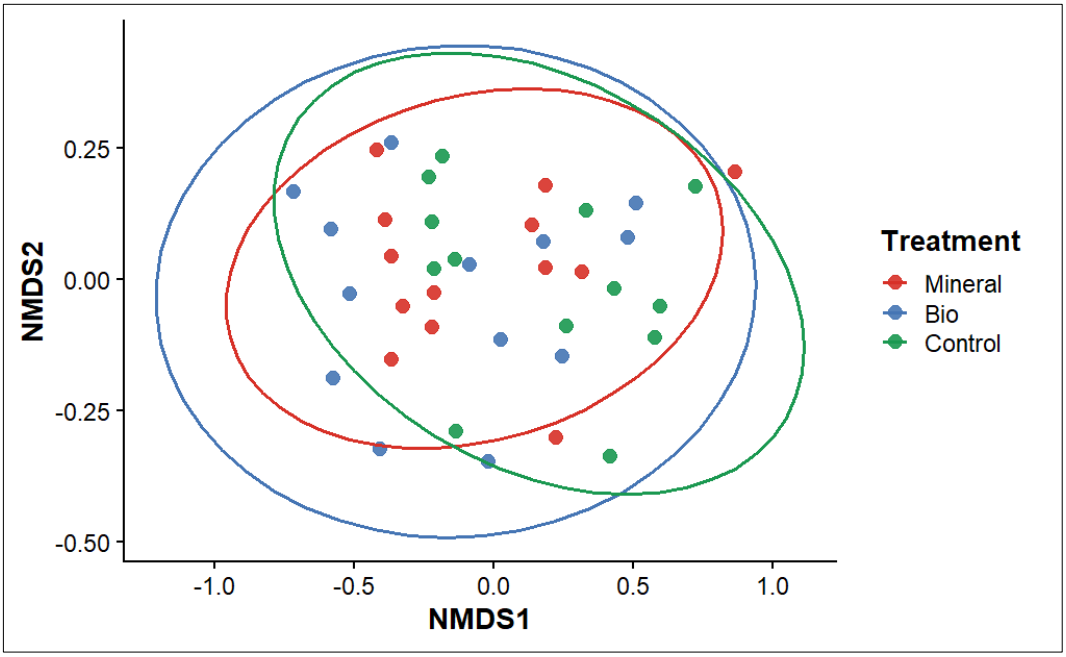


Figure 5: Non-metric multidimensional scaling (NMDS) of understory vegetation community composition under three long-term fertilization treatments in northern Swedish boreal forests (n = 13 treatment areas per treatment). Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. Each point represents one treatment-area community, based on square-root-transformed mean species cover and Bray–Curtis dissimilarities. Ellipses represent 95% confidence regions for each treatment group. NMDS stress = 0.109. Treatment effects on community composition were tested using PERMANOVA with 9,999 permutations restricted within sites.

3.4 Functional-group responses to fertilization

Mean cover differed significantly among treatments for four of the seven functional groups after BH-FDR correction (Figure 6). Dwarf-shrub cover was highest in control stands, compared with mineral-fertilized and biofertilized stands, with both treatments differing significantly from controls. Graminoid cover showed the opposite pattern, being higher under mineral fertilization and biofertilization than in controls. Forb cover was highest under biofertilization, followed by mineral fertilization and controls, with significant differences between all three treatments. Ground lichen cover was also significantly affected, being highest in controls and considerably lower under mineral fertilization and biofertilization. Bryophytes, shrubs and ferns showed no significant treatment effects on mean cover.

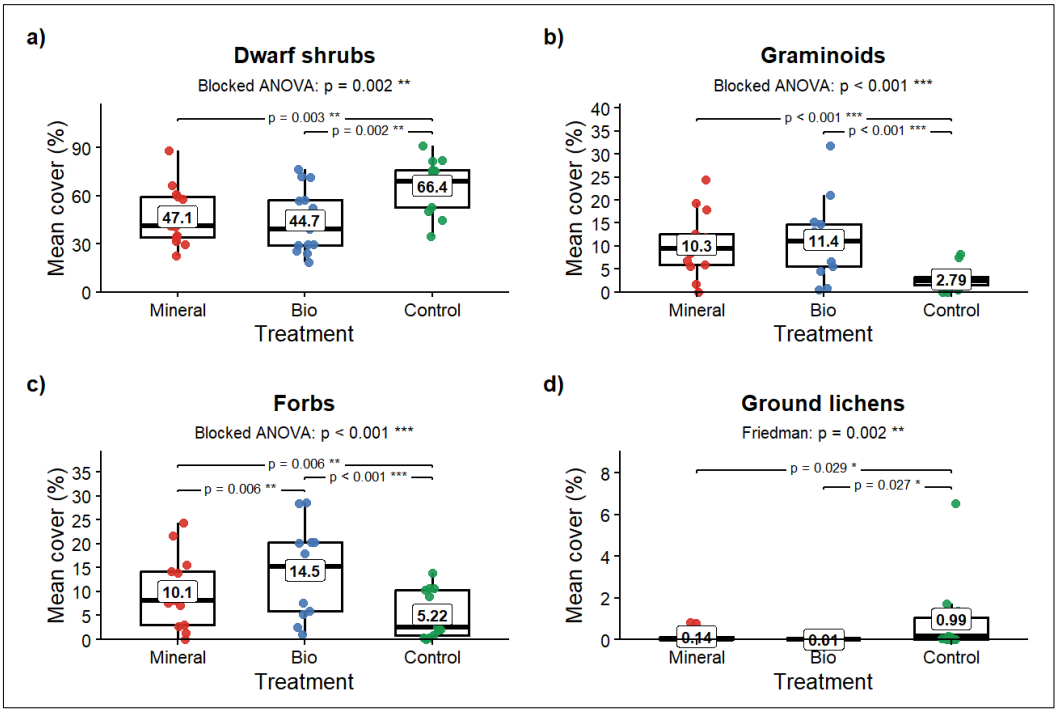


*Figure 6: Effects of long-term forest fertilization on mean cover of understory functional groups showing significant treatment responses in northern Swedish boreal forests (n = 13 treatment areas per treatment). Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. Points represent treatment areas. Boxes show the interquartile range (25th–75th percentiles), horizontal lines indicate medians, whiskers extend to 1.5 times the interquartile range, and numerical labels indicate means. Overall effects were tested using blocked ANOVA or Friedman tests, with BH-FDR correction across functional groups. Brackets show Holm-adjusted pairwise comparisons (*p < 0.05, **p < 0.01, ***p < 0.001).*

Functional-group occurrence also differed among treatments (Figure 7). Graminoids occurred in a higher proportion of plots under mineral fertilization and biofertilization than in controls. Forb occurrence was highest under biofertilization, followed by mineral fertilization and controls, with significant differences between all treatments. Ground lichen occurrence was highest in controls, followed by mineral-fertilized and biofertilized stands. Bryophytes, dwarf shrubs, shrubs and ferns showed no significant pairwise treatment differences after Holm adjustment.

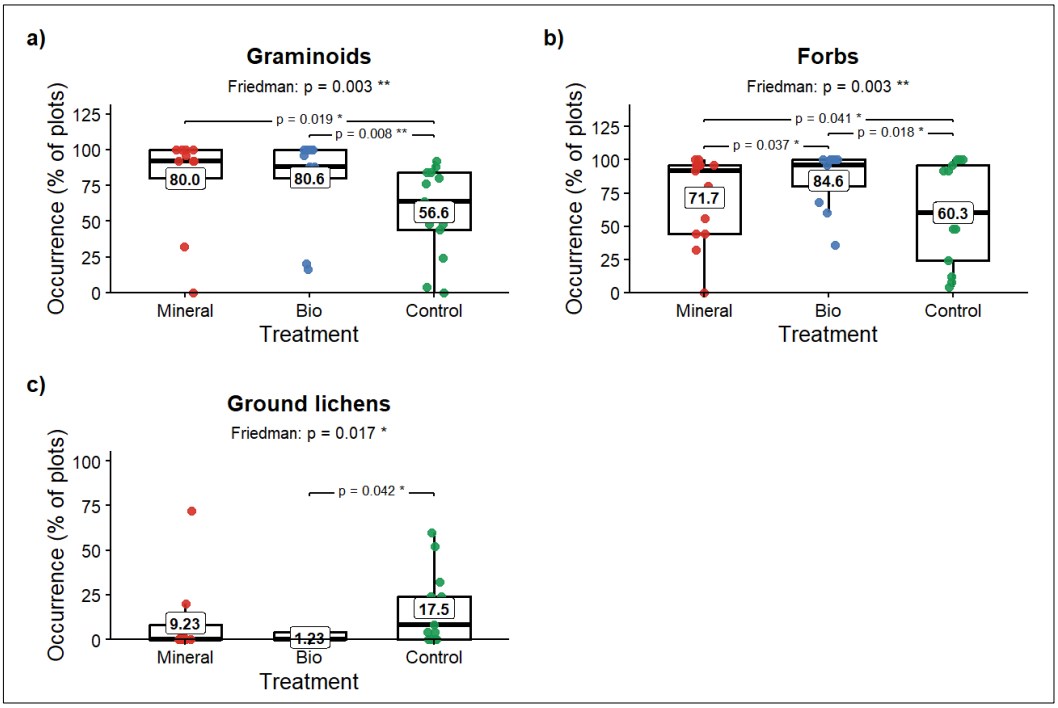


*Figure 7: Effects of long-term forest fertilization on functional-group (at least one species within the group) occurrence in northern Swedish boreal forests (n = 13 treatment areas per treatment). Occurrence represents the percentage of plots containing at least one species from each group. Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. Points represent treatment areas; boxes show the interquartile range (25th–75th percentiles), horizontal lines indicate medians, whiskers extend to 1.5 times the interquartile range, and numerical labels show means. Treatment effects were tested using Friedman tests with BH-FDR correction across functional groups. Brackets show Holm-adjusted pairwise comparisons (*p < 0.05, **p < 0.01, ***p < 0.001).*

3.5 Species-level response to fertilization

Species-level responses were predominantly detected between biofertilized and control stands (Figure 8). Biofertilization significantly increased mean cover of *Avenella flexuosa*, *Chamaenerion angustifolium* (rosebay willowherb), *Luzula pilosa* (hairy wood-rush), *Maianthemum bifolium* (false lily-of-the-valley) and *Linnaea borealis* (twinflower), while *Vaccinium vitis-idaea* decreased significantly. Occurrence was also higher under biofertilization for *A. flexuosa*, *C. angustifolium*, *L. pilosa* and *Solidago virgaurea* (European goldenrod). Conditional cover increased for *A. flexuosa*, *M. bifolium* and *Melampyrum sylvaticum* (small cow-wheat), while *V. vitis-idaea* decreased. Species-level responses to mineral fertilization were more limited. Compared with controls, conditional cover increased for *A. flexuosa* and decreased for *V. vitis-idaea*, while no significant differences in mean cover or occurrence were detected. The Bio-Mineral comparison identified only one significant difference, with higher mean cover of *C. angustifolium* under biofertilization.

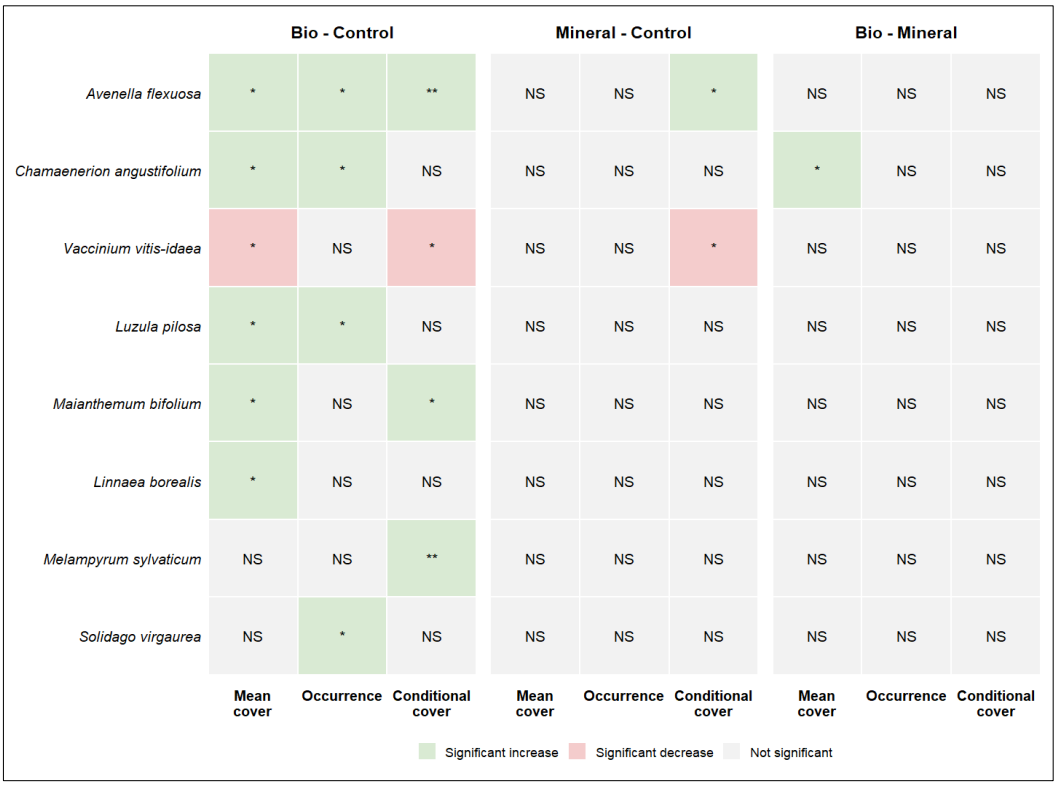


*Figure 8: Species-level responses to long-term fertilization in northern Swedish boreal forests (n = 13 sites per treatment), showing differences in mean cover, occurrence and conditional cover. Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. Contrasts were tested using exact paired randomization tests with BH-FDR correction within each response × contrast. Green indicates significant increases, red significant decreases and grey non-significant differences (*p < 0.05, **p < 0.01; NS = not significant). Species that did not differ for any of the tests between treatments are not displayed.*

3.6 Community-weighted ecological indicator values

Community-weighted nitrogen indicator values were significantly different among treatments (Figure 9a). Treatment explained a large proportion of the variation (partial $\eta^2 = 0.59$, $p < 0.001$). Biofertilized stands exhibited the highest mean nitrogen indicator value (2.99), followed by mineral-fertilized stands (2.73) and control stands (2.17). Holm-adjusted pairwise comparisons showed that both fertilized treatments differed significantly from the control (Bio–Control: $p < 0.001$; Mineral–Control: $p < 0.001$). Mineral and biofertilization did not differ significantly ($p = 0.080$).

Community-weighted phosphorus indicator values also differed significantly among treatments, although the effect size was smaller (partial $\eta^2 = 0.26$, $p = 0.025$) (Figure 9b). Biofertilized stands showed the highest mean value (2.95), followed by mineral-fertilized (2.85) and control stands (2.82). Holm-adjusted pairwise comparisons revealed that only the comparison between biofertilized and control stands remained significant ($p = 0.029$).

Community-weighted light indicator values also differed significantly among treatments (Figure 9c), with a large treatment effect (partial $\eta^2 = 0.47$, $p < 0.001$). Control stands exhibited the highest mean light indicator value (4.11), followed by mineral-fertilized stands (3.87) and biofertilized stands (3.72). Holm-adjusted pairwise comparisons showed that both fertilized treatments differed significantly from the control (Bio–Control: $p < 0.001$; Mineral–Control: $p = 0.015$). Mineral and biofertilization did not differ significantly ($p = 0.123$).

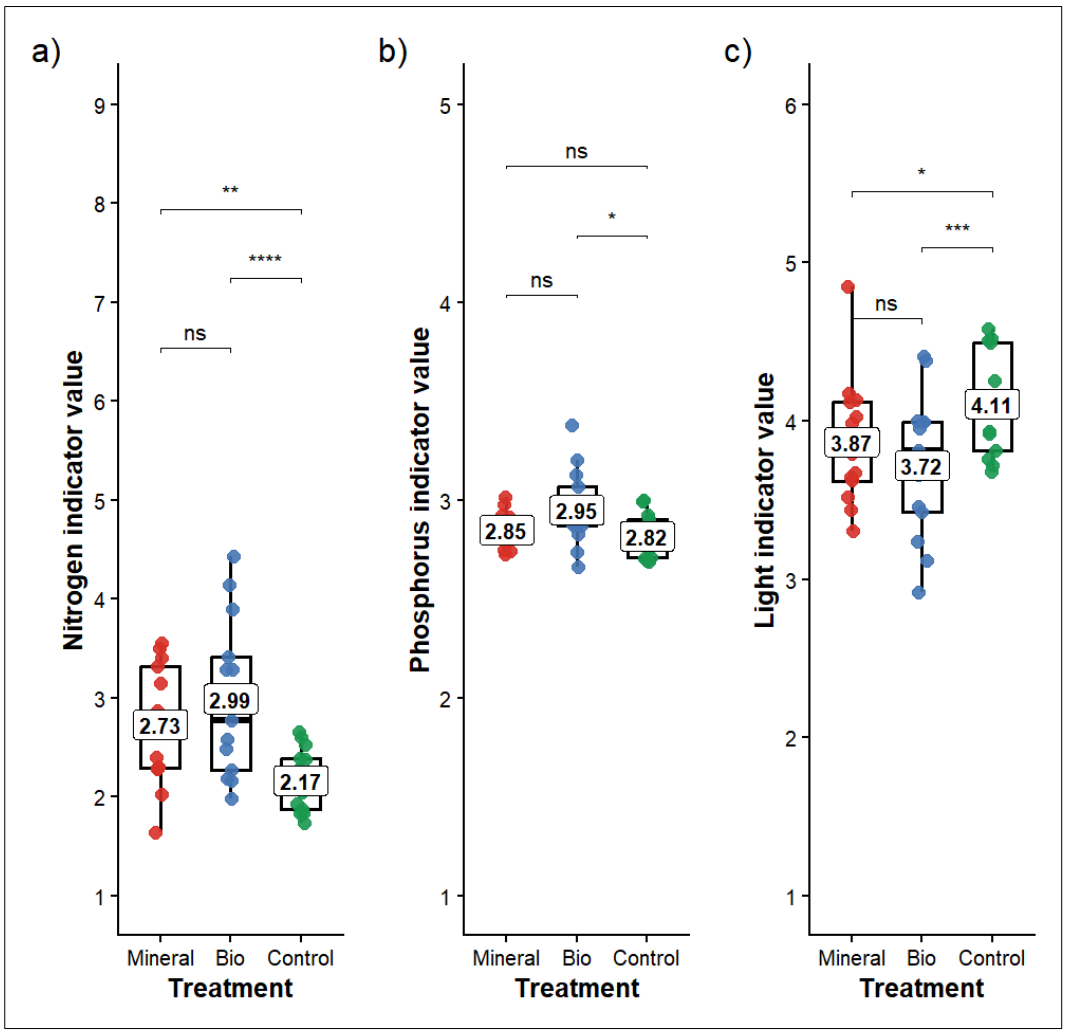


*Figure 9: Community-weighted mean (CWM) ecological indicator values for (a) nitrogen, (b) phosphorus and (c) light under long-term forest fertilization in northern Swedish boreal forests (n = 13 sites per treatment). Bio = biofertilized; Mineral = mineral-fertilized; Control = unfertilized. CWM values were calculated using Tyler et al. (2021), weighted by mean vascular-plant cover. Points represent treatment areas; boxes show the interquartile range (25th–75th percentiles), horizontal lines indicate medians, whiskers extend to 1.5 times the interquartile range, and numerical labels show means. Treatment effects were tested using site-blocked ANOVA with Holm-adjusted pairwise comparisons (ns = not significant, *p < 0.05, **p < 0.01, ***p < 0.001).*

3.7 Environmental covariates

The relative importance of fertilization and environmental covariates was assessed separately for species richness and community composition. For richness, predictor contributions represent changes in explained variation when each variable was excluded from the full model. For community composition, contributions represent variation explained by each predictor after accounting for the others.

Fertilization remained the strongest independent predictor of plot-scale species richness after accounting for environmental covariates (Figure 10a). Removing treatment reduced marginal R^2 by 10.11 percentage points (from 39.9% to 29.8%), followed by dominant tree group (4.26 percentage points), stand age (3.31) and latitude (3.27). The remaining covariates each contributed between 0.15 and 1.12%. The full model explained 39.9% of richness variation through fixed effects and 53.5% when random effects were included. Significant main effects were detected for treatment ($F = 30.08$, $p < 0.001$), dominant tree group ($F = 12.50$, $p < 0.001$), latitude ($F = 6.73$, $p = 0.032$) and soil moisture ($F = 4.23$, $p = 0.006$).

Fertilization also explained significant variation in community composition after accounting for environmental covariates (Figures 10b–c). For Bray–Curtis dissimilarity, treatment accounted for 8.05% of compositional variation ($p < 0.001$), while soil moisture accounted for 2.61% ($p = 0.030$). For Jaccard dissimilarity, treatment was the only significant predictor ($R^2 = 5.53\%$, $p = 0.003$). None of the remaining environmental covariates showed significant independent effects on community composition.

Stand age was the only environmental covariate that significantly modified the relationship between treatment and species richness ($F_{2,21.9} = 8.41$, $p = 0.014$; Figure 11). Richness showed no significant relationship with stand age in controls (−0.004 species/year, $p = 0.832$). However, it decreased with increasing stand age under mineral fertilization (−0.053 species/year, $p = 0.015$) and biofertilization (−0.042 species/year, $p = 0.043$). The slopes differed significantly between controls and mineral fertilization (Tukey-adjusted $p = 0.002$) and between controls and biofertilization ($p = 0.016$), but not between the two fertilization treatments ($p = 0.659$). Thus, the positive richness response to fertilization was higher in younger than in older stands across the observed stand-age gradient. No other treatment × covariate interactions were significant for species richness.

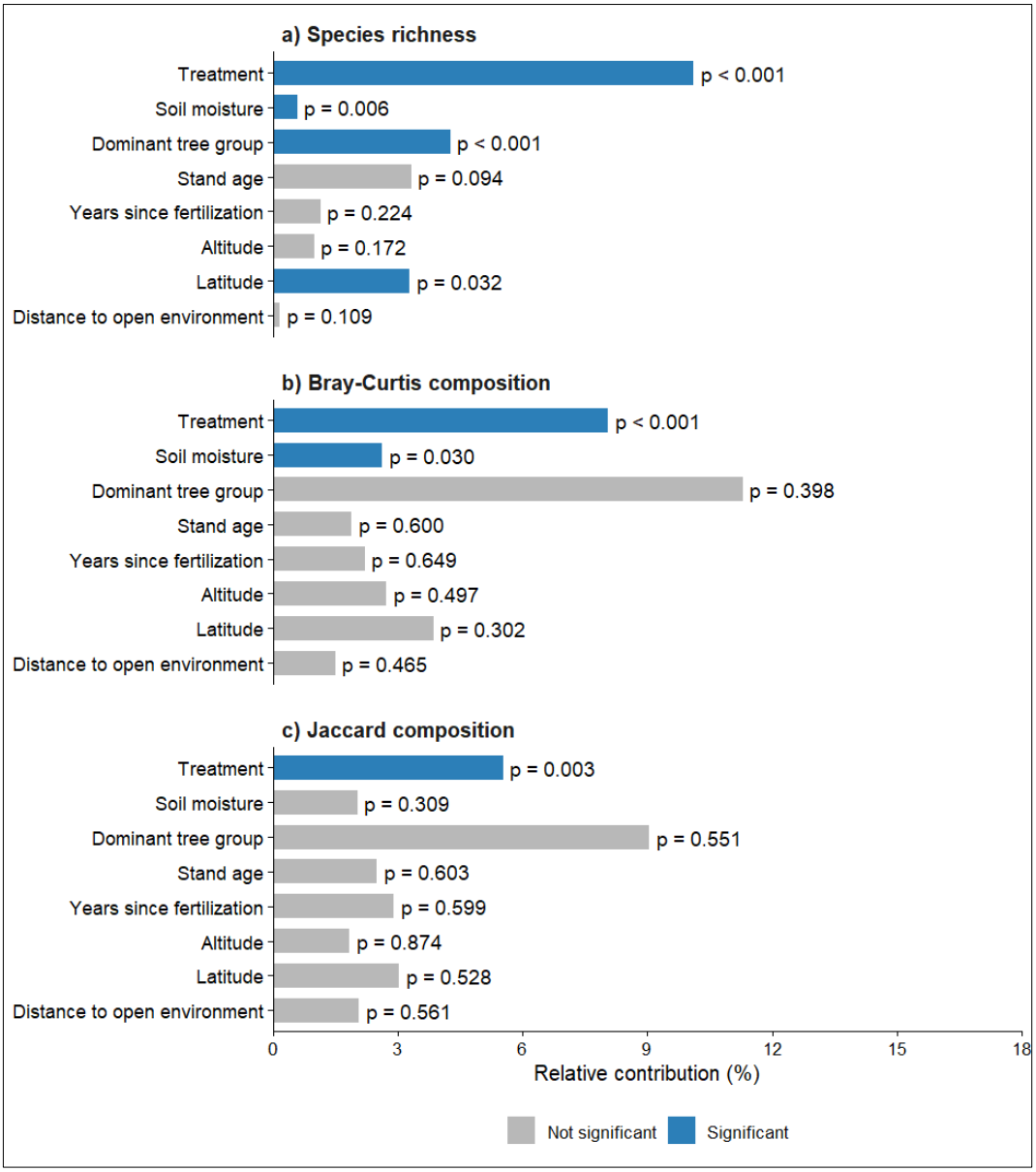


Figure 10: Relative contribution of fertilization treatment and environmental covariates to (a) plot-scale species richness, (b) Bray–Curtis community composition, and (c) Jaccard community composition in northern Swedish boreal forests. Treatments were Bio = biofertilized, Mineral = mineral fertilizer application, and Control = no fertilizer applied; treatments were established 18–20 years before sampling, with 13 sites per treatment. For species richness, bars show the reduction in marginal R^2 when each predictor was removed from the full linear mixed-effects model, which included site, treatment area within site, and transect within treatment area as random effects. Main effects were tested using Type II Wald F-tests with Kenward–Roger adjustment. The stand age × treatment interaction was significant (BH-adjusted $p = 0.014$), although the main effect of stand age was not. For community composition, bars show marginal PERMANOVA R^2 from models including treatment and all environmental covariates simultaneously, based on Bray–Curtis dissimilarities of square-root-transformed mean species cover and Jaccard dissimilarities of presence–absence data. PERMANOVA tests used 9,999 permutations with permutation structure matched to the spatial level of each predictor. Blue bars indicate significant effects; grey bars indicate non-significant effects.

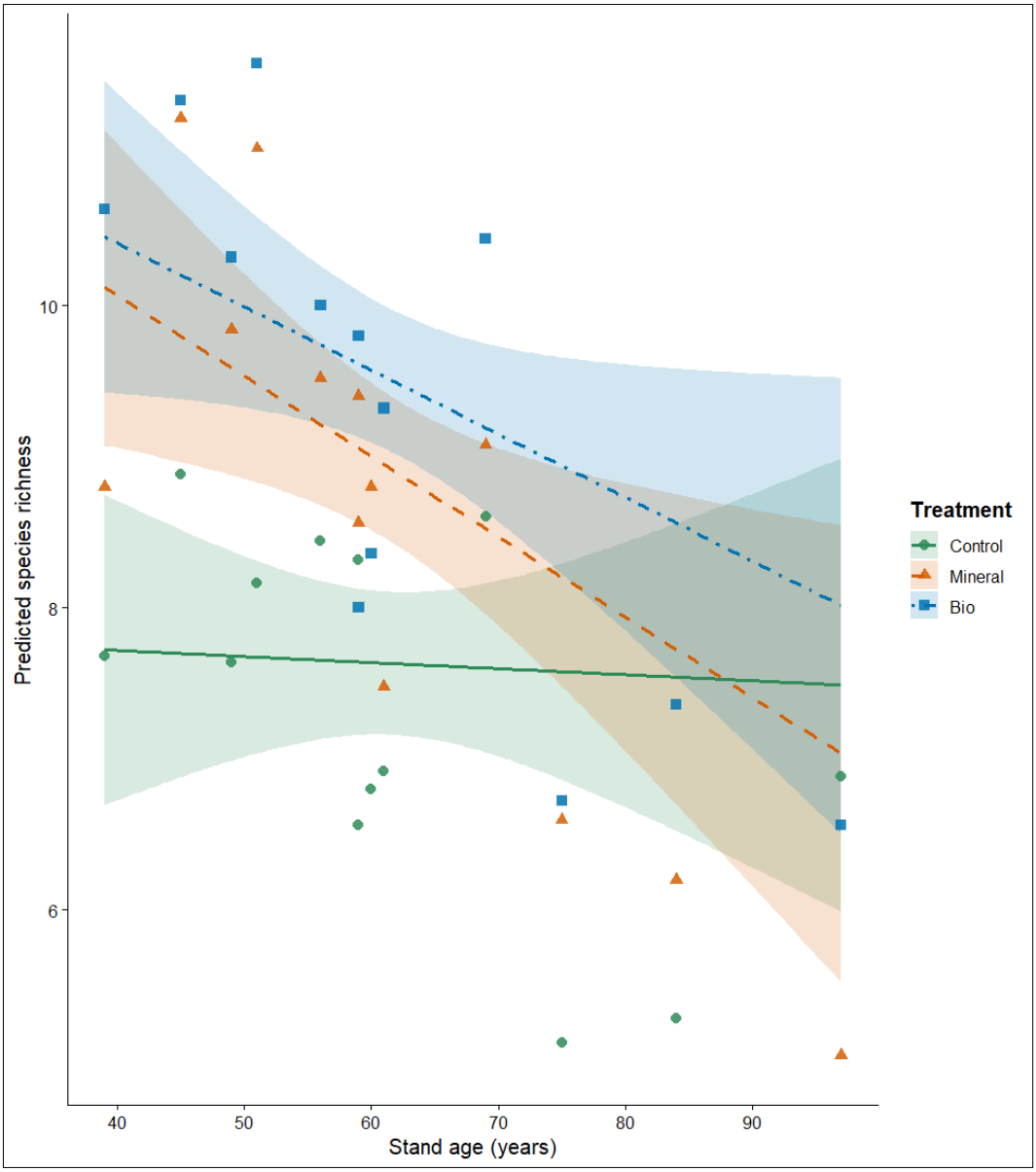


Figure 11: Relationship between stand age and predicted plot-scale species richness under three long-term fertilization treatments in northern Swedish boreal forests. Treatments were Bio = biofertilized, Mineral = mineral fertilizer application, and Control = no fertilizer applied; treatments were established 18–20 years before sampling, with 13 sites per treatment. Lines show model-predicted species richness across the observed stand-age gradient, shaded areas represent 95% confidence intervals, and points show observed mean richness for each site × treatment combination. Predictions were obtained from a linear mixed-effects model including treatment, stand age, their interaction, and the remaining environmental covariates, with site, treatment area within site, and transect within treatment area included as random effects. The treatment × stand age interaction was significant ($F_{2,21.9} = 8.41$, raw $p = 0.002$, BH-adjusted $p = 0.014$). Richness was negatively associated with stand age in both fertilized treatments, but not in controls.

3.8 Synthesis of the results

Treatment effects were detected across several components of the understory vegetation, although the magnitude and direction of responses varied among variables and between fertilization treatments. Table 3 summarizes the main results, with treatment responses expressed relative to the unfertilized control.

Table 3: Summary of understory vegetation responses to mineral and biofertilization relative to control stands. ↑ represents an increase compared to control, ↓ represents a decrease compared to control and ↔ means no significant difference.

Response variable	Mineral Control	Bio Control	Treatment pattern
Plot-scale species richness	↑	↑	Bio > Mineral > Control
Treatment-area species richness	↑	↑	Bio > Mineral > Control
Bray-Curtis community composition	Different	Different	Treatment R^2 = 9.2%
Jaccard community composition	↔	Different	Treatment R^2 = 5.7%
Bray-Curtis beta diversity	↔	↔	No treatment effect
Jaccard beta diversity	↔	↔	No treatment effect
Dwarf shrub cover	↓	↓	Control > Mineral ≈ Bio
Dwarf shrub occurrence	↔	↔	No treatment effect
Graminoid cover	↑	↑	Bio ≈ Mineral > Control
Graminoid occurrence	↑	↑	Bio ≈ Mineral > Control
Forb cover	↑	↑	Bio > Mineral > Control
Forb occurrence	↑	↑	Bio > Mineral > Control
Ground lichen cover	↓	↓	Control > Mineral ≈ Bio
Ground lichen occurrence	↔	↓	Control > Bio
Other functional groups: bryophytes, shrubs, ferns	↔	↔	No treatment effect
Species-level responses	Limited	Stronger	Responses concentrated in Bio–Control
CWM nitrogen	↑	↑	Bio ≈ Mineral > Control
CWM phosphorus	↔	↑	Bio > Control
CWM light	↓	↓	Bio ≈ Mineral < Control

4. Discussion

This study investigated the long-term effects of mineral (SkogCan) and organic (bionäring) fertilization on understory vegetation in northern Swedish boreal forests, ~20 years after the initial treatment. By comparing mineral and wastewater-derived organic fertilization within the same study system, this study extends previous research focused mainly on conventional mineral fertilizers and provides evidence of treatment-associated vegetation differences 18–20 years after the initial nutrient addition was performed. The results showed that fertilization still influenced several aspects of understory vegetation, although the direction and magnitude of these responses differed among vegetation analyses and fertilization treatments.

Contrary to the initial expectation of reduced species richness (H1), both fertilization treatments were associated with higher richness. Fertilization also significantly altered community composition, although no significant differences in within-area beta diversity were detected. As hypothesized, fertilization favoured graminoids and forbs, reduced dwarf-shrub and ground lichen cover, whereas bryophyte cover showed no significant response. The differences between mineral and organic fertilization (H1) were smaller than expected. Although biofertilization generally produced stronger responses, direct differences between the two treatments were often not significant. Changes in community-weighted ecological indicator values further suggested shifts in the ecological affinities of understory vegetation (H2). Both fertilization treatments increased nitrogen indicator values and decreased light indicator values relative to controls, while phosphorus indicator values increased significantly only under biofertilization. As hypothesized, fertilization remained an important predictor of species richness and community composition after accounting for environmental covariates (H3). Dominant tree group and soil moisture also influenced richness, while stand age modified the richness response to fertilization, with stronger positive responses in younger stands. Below, these findings and their ecological implications are discussed in detail.

4.1 Sampling completeness

The completeness estimate was moderate (72.9 to 84.2%) but comparable to levels reported in other forest vegetation studies using incidence-based richness estimators (Chao et al. 2020; Reeve et al. 2022). The incompleteness was likely driven by a relatively high proportion of species occurring in only a single site within treatment (25-28% of the total recorded species depending on the treatment), as richness estimators such as Chao2 are sensitive to rare species because they rely

strongly on their frequency (Chao 1987). Although the Chao2 estimator suggested that the total treatment-level richness was only partially complete, the accumulation curves suggest that the common species in the community were well represented. Additional sampling would therefore be expected to primarily increase total species richness or site-scale species richness through the detection of rare and spatially restricted taxa. The main-community-level analyses in this study, including community composition, functional-group responses and relationships with environmental covariates, were based on treatment-level communities (n = 39) and are consequently less dependent on exhaustive detection of rare species. Furthermore, species occurring too infrequently across sites could not provide sufficient replication for the species-level analyses.

4.2 Species richness response to fertilization

Fertilization had a positive effect on understory species richness, with both plot and treatment-area scales following the same pattern, with the highest richness under biofertilization followed by mineral fertilization and control treatments. These findings contrast with previous studies where richness responses to fertilization have been neutral or negative. Sullivan & Sullivan (2018) reviewed the effects of mineral fertilization on vegetation diversity and found that the responses are not uniform, but that in most cases fertilization tends to decrease or have no effect at all on plant richness, which contrasts with the increased species richness observed in the present study. For instance, in an experimental study that combined thinning and fertilization, the treatment did not have an influence on understory plant and bryophyte richness, but it changed composition (Hedwall et al. 2013b). The same conclusion was made by Xing et al. (2019) in a Chinese boreal forest. In the case of a study conducted by Kellner & Mårshagen (1991), understory species richness increased after seven years of irrigation and fertilization on the ground vegetation in a 130-year-old stand of Scots pine. In contrast, Turkington et al. (2002), who conducted a study on fertilization and herbivory on herbaceous vegetation reported a reduction in species richness after a 10-year survey. The experimental design assessed in the present study is particularly difficult to compare to other studies as many of them combined fertilization with the modification of another environmental covariate such as irrigation (Kellner & Mårshagen 1991), thinning (Hedwall et al. 2013b) and herbivory (Turkington et al. 2002) or/and did not feature the same temporal trajectory. The present study provides evidence that forest fertilization alone can increase understory species richness, even ~20 years after nutrient addition.

As plant growth in boreal forests is commonly limited by low nutrient availability, particularly nitrogen (Tamm 1991; Näsholm et al. 1998; Boonstra et al. 2017), fertilization may have reduced nutrient limitation and favoured the

establishment or persistence of more nutrient-demanding species. However, nutrient enrichment does not necessarily increase species richness. Increased nutrient availability can favour fast-growing, competitive species, potentially leading to the exclusion of slower-growing species, particularly through increased competition for light (Hautier et al. 2009). Sullivan and Sullivan (2018) reported that understory species richness increases were occasionally observed in initially species-poor and unproductive forests. The higher richness observed in the present study may therefore indicate that nutrient enrichment allowed additional species to coexist with the original understory vegetation, rather than causing competitive exclusion. This interpretation is consistent with the increased occurrence of forbs and graminoids under fertilization, alongside the persistence of characteristic dwarf shrubs. Nevertheless, the significant changes in community composition and reductions in ground-lichen cover indicate that fertilization also disadvantaged some components of the original vegetation. Thus, increased species richness did not necessarily reflect an overall improvement in understory biodiversity, but rather a shift in community structure favouring certain ecological groups.

Biofertilized stands had significantly higher species richness at both plot and treatment-area scales than mineral-fertilized stands. One possible explanation is the difference in total nutrient input between treatments. Although mineral-fertilized stands received two applications, resulting in a cumulative input of approximately 292 kg N/ha, this remained substantially lower than the average 532 kg N/ha and the additional P, K, Ca, Mg applied through biofertilization (Sahlén 2012). The higher input under biofertilization may therefore have contributed to a stronger and more persistent reduction in nutrient limitation, allowing additional species to establish or persist. However, the difference in fertilizer composition and nutrient release dynamics may also help explain the observed richness patterns. The majority of nitrogen in sewage sludge is organically bound (Lindberg et al. 2013) and must undergo microbial mineralization before becoming available to plants (Sahlén et al. 2011; Kirchmann et al. 2017). This can result in more gradual nutrient release compared with conventional mineral fertilizers (Näslund 2015; Kominko et al. 2017). Consequently, biofertilization may have provided a more prolonged supply of nutrients, potentially favouring the establishment or persistence of nutrient-demanding understory species over time. However, it is unclear whether nutrient release continued until sampling or whether the observed vegetation differences reflect lasting effects of earlier nutrient enrichment. Both the higher nutrient input and differences in nutrient-release dynamics could therefore have contributed to the higher species richness observed under biofertilization. However, because fertilizer types, nutrient quantity, composition and release rates differed simultaneously, the contributions of individual components of each of the treatments could not be distinguished.

4.3 Community structure response to fertilization

Fertilization significantly altered community composition, although no significant treatment effects on within-area beta diversity were detected. Biofertilized areas showed slightly lower mean beta diversity than mineral-fertilized and control areas for both Bray–Curtis and Jaccard dissimilarities, but these differences were not statistically significant. This contrasts with Hedwall et al. (2011), who reported reduced variation in understory composition following repeated fertilization in Norway spruce stands. Differences in fertilization intensity, forest characteristics and time since treatment may partly explain these contrasting findings. Nevertheless, unchanged beta diversity does not imply that species composition remained unaffected. Jaccard PERMANOVA detected a significant treatment effect where fertilization explained 5.7% of the compositional variation. Biofertilized communities differed significantly from controls, whereas mineral-fertilized communities did not. Thus, biofertilization was associated with detectable changes in species presence-absence without significantly changing the heterogeneity of species assemblages within treatment areas.

Bray-Curtis PERMANOVA, which also accounts for variation in species cover, detected significant differences between both fertilization treatments and controls, with treatment explaining 9.2% of compositional variation. This suggests that changes in relative species cover contributed to community restructuring, even where changes in species presence-absence were less pronounced. Such responses are consistent with Strengbom et al. (2001), who reported persistent changes in understory composition and abundance following nitrogen fertilization, including increased *Avenella flexuosa* and decreased *Vaccinium myrtillus*. Similarly, Hedwall et al. (2021) identified nitrogen deposition and forest density as important drivers of long-term understory vegetation changes in Sweden, including declining dwarf-shrub cover. The increased cover of graminoids and forbs together with the reduced dwarf-shrub cover observed in the present study further agree with findings from Hedwall et al. (2010), Xing et al. (2019) and Jetsonen et al. (2024). However, biofertilized and mineral-fertilized communities did not differ significantly from each other, and treatment explained a relatively small proportion of overall compositional variation. Multivariate dispersion also remained unchanged, supporting the interpretation that PERMANOVA detected shifts in community rather than differences in dispersion.

The relatively small proportion of variation explained by fertilization suggests that other factors, such as site history, environmental heterogeneity and species interactions were the main drivers that shaped community composition. Nevertheless, treatment effects remained detectable after approximately two decades after initial fertilization.

4.4 Functional groups and species responses to fertilization

Fertilization affected the understory functional groups differently, with increased cover of forbs and graminoids and decreased cover of dwarf shrubs and ground lichens. These findings support the functional-group predictions of the first hypothesis, although bryophyte cover did not change significantly. Similar changes have been reported following nitrogen enrichment in boreal forests, where increased nutrient availability favoured herbaceous vegetation while reducing the abundance of dwarf shrubs (Strengbom & Nordin 2008; Hedwall et al. 2011; Xing et al. 2019; Jetsonen et al. 2024). The persistence of these differences ~20 years after the initial fertilization is also consistent with Olsson and Kellner (2006), who observed long-lasting changes in understory vegetation 15-18 years after nitrogen addition ceased. However, the inclusion of biofertilization in the present study further demonstrates that organic nutrient addition can produce similar long-term changes in functional composition to those previously documented for mineral fertilization. The simultaneous increase in graminoids and forbs and decrease in dwarf shrubs may result from several interacting mechanisms. Increased nutrient availability can favour species capable of exploiting additional nutrients, while also modifying competitive relationships within the understory. Fertilization may additionally affect vegetation indirectly by stimulating tree growth, increasing litter production and altering light availability beneath the canopy. Manninen et al. (2009) reported a reduced biomass for *Vaccinium myrtillus* and increased abundance for *Avenella flexuosa* and graminoids in general following nitrogen addition in northern Finnish boreal forests. Similarly, Hedwall et al. (2013a) observed a long-term shift from dwarf shrub towards grasses and ferns in fertilized Norway spruce forests, accompanied by reduced below-canopy light availability. These studies suggest that both changes in resource availability and indirect effects of fertilization on forest structure could have contributed to the shifts observed in the present study. The decline in dwarf-shrub cover was particularly associated with *Vaccinium vitis-idaea*, which showed lower abundance in both fertilized communities. Negative responses of *Vaccinium* species to nutrient enrichment have previously been documented in the boreal forest (Strengbom & Nordin 2008; Manninen et al. 2009; Jetsonen et al. 2024; Männistö et al. 2026). Experimental evidence suggests that nitrogen addition can influence the physiology and C/N balance of *Vaccinium* shrubs (Palmroth et al. 2014). However, the decrease observed here cannot be attributed exclusively to a direct physiological response to increased nutrient availability, as altered competition and canopy development may also have contributed.

In contrast, several graminoid and forb species benefited from fertilization, particularly under biofertilization. *Avenella flexuosa* showed the clearest positive

response, consistent with its previously documented ability to benefit from nitrogen addition in boreal forests (Manninen et al. 2009). However, such responses are not universal, as Männistö et al. (2026) reported that the response of *A. flexuosa* to nitrogen enrichment can vary depending on forest conditions and fertilization intensity. Several forbs, including *C. angustifolium, M. bifolium, M. sylvaticum* and *S. virgaurea*, also responded positively to biofertilization. These changes suggest that nutrient enrichment favoured certain species associated with more productive understory conditions rather than producing a uniform increase across all species within the same functional group. This interpretation is supported by the community-weighted ecological indicator analysis, which revealed higher nitrogen indicator values in both fertilized treatments and higher phosphorus indicator values under biofertilization compared with controls. Some species, such as *C. angustifolium* have high nitrogen and phosphorus indicator values, while *V. vitis-idaea* is associated with nutrient-poor environments (Tyler et al. 2021). The contrasting responses of these species therefore contributed to a broader shift toward vegetation characteristic of more nutrient-rich conditions. Hedwall et al. (2017) have documented similar changes in Swedish boreal forests where combined nitrogen and phosphorus addition promoted more mesotrophic vascular plant communities. This is particularly relevant given that organic fertilization contained a substantial amount of phosphorus.

However, the functional-group responses were not equally pronounced for all vegetation analyses. Bryophyte cover did not differ significantly among treatments, despite previous studies reporting negative responses to nitrogen enrichment (Xing et al. 2019; Jetsonen et al. 2024). Bryophyte responses may depend on species identity and fertilization intensity. Dirkse and Martakis (1992) observed decreases in glittering wood-moss (*Hylocomium splendens*) and red-stemmed feather-moss (*Pleurozium schreberi)* under elevated nitrogen inputs, while some *Brachythecium* species increased at lower fertilization levels. Although similar descriptive patterns with a lower cover in fertilized stands were observed for some bryophytes in the present study (Appendix 15), no individual bryophyte species showed a statistically significant treatment response. This suggests that the long-term effects of fertilization were less pronounced or less consistent for bryophytes than for vascular plants, which is also consistent with Hedwall et al. (2017).

Ground lichens showed clear negative responses to fertilization. Cover was lower under both mineral and biofertilization, while occurrence was significantly lower under biofertilization than in controls. Although biofertilized stands had the lowest mean lichen cover and occurrence, differences between the two fertilizer treatments were not statistically significant. These findings are consistent with previous studies reporting reductions in ground lichens following forest fertilization (Olsson & Kellner 2006; Strengbom & Nordin 2008). Olsson and Kellner (2006) documented reductions in the abundance of certain lichen taxa 15-18 years after

nitrogen addition. The present results extend these observations by showing that not only mineral fertilization, but also organic biofertilization can be associated with long-term reductions in ground lichens. However, because lichens were not identified to species level, it is not possible to determine whether the observed reduction is driven by certain taxa or whether the reduction is widespread across ground-lichen taxa. Several mechanisms could explain the negative responses of ground lichens. Nutrient enrichment may affect lichens directly, although their nutritional ecology differs from that of vascular plants because they acquire much of their nutrients from atmospheric sources (Hauck 2010; Carter et al. 2017). Responses to nitrogen enrichment can also vary among lichen groups. Johansson et al. (2010) documented positive responses among certain epiphytic lichens, although these findings cannot be directly extrapolated to ground-dwelling species. Increased vascular-plant growth can intensify competition for space and light, while stimulated tree growth may increase canopy shading and needle litterfall, further reducing favourable conditions for ground lichens (Jonsson et al. 2021; Tonteri et al. 2022; Jetsonen et al. 2024; Roos et al. 2025).

The lower community-weighted light indicator values observed under both fertilization treatments are consistent with a shift toward vegetation associated with more shaded environments. However, because light availability, canopy openness or basal area were not directly measured, the relative importance of these mechanisms cannot be established. The simultaneous increase in vascular-plant cover and reduction in ground lichens suggests that changes in the vegetation structure and competitive conditions may have contributed to the observed lichen responses. Ground lichens were relatively scarce even in the unfertilized control areas, which should be considered when interpreting these findings. Lichen-rich vegetation is commonly associated with nutrient-poor forest conditions (Tonteri et al. 2022), whereas forest stands selected for fertilization are generally those expected to respond favourably in terms of tree growth. In addition, lichen-rich stands are often excluded from forest fertilization, with further consideration given to areas important for reindeer husbandry (Kivinen et al. 2010). The low abundance of ground lichens in the study areas therefore limits the extent to which the observed reductions can be generalized to lichen-rich forests. Nevertheless, lichens represent an important component of boreal forest ecosystems, contributing to ecological processes and biodiversity (Asplund & Wardle 2017). Terricolous lichens constitute an important winter forage resource for reindeer, and their abundance and accessibility influence the suitability of forest stands for winter grazing (Kater & Baxter 2022; Eggers et al. 2024). Although the relatively low lichen abundance in the present study does not allow conclusions about effects on reindeer forage availability, the broader decline of ground lichens remains a significant concern for reindeer husbandry. In Sweden, ground-lichen cover declined by approximately 57% between 1996 and 2015 (Roos et al. 2025).

4.5 Environmental covariates

The third hypothesis, which was that fertilization would influence understory richness and community composition independently of variation in environmental conditions, was supported. Fertilization remained a significant predictor for both species richness and community composition after accounting for the measured environmental covariates. For plot-scale richness, treatment had the largest independent explanatory contribution, indicating that the higher richness observed in fertilized plots could not be explained solely by differences in soil moisture, dominant tree group, stand age or geographical conditions. Although some of the measured environmental variables also contributed to variation in understory vegetation, fertilization remained the most consistent predictor of long-term differences among treatments.

Dominant tree group and soil moisture also significantly influenced species richness, consistent with their established importance for understory vegetation. Scots pine dominated plots supported a lower richness than Norway spruce dominated and mixed plots. Similar differences have been reported in southern Sweden, where Norway spruce-dominated stands supported a higher understory richness than Scots pine-dominated stands (Petersson et al. 2019). Petersson et al. (2019) suggested that the higher abundance of dwarf shrubs in Scots pine stands may competitively suppress other vascular plants, while dominant tree species can also influence understory vegetation through differences in canopy structure, litter inputs and associated soil conditions (Barbier et al. 2008). Soil moisture significantly influenced species richness, although its independent explanatory contribution was small. Its importance for vascular-plant and bryophyte richness has previously been demonstrated in boreal forests (Koelemeijer et al. 2024). Latitude also showed a significant association with species richness, contributing 3.27% to marginal R^2. This association is consistent with the literature (Grytnes et al. 2008) and shows that geographical variation influences understory richness even within the relatively restricted latitudinal range of this study. However, the association may reflect unmeasured environmental gradients rather than a direct effect of latitude. Other environmental covariates, including altitude, did not significantly affect richness. Although altitude has been associated with plant diversity at broader spatial scales (Grytnes et al. 2006), the relatively narrow altitudinal range represented in this study may explain its limited influence.

Although the main effect of stand age on richness was not significant, it significantly modified the fertilization response. Richness declined with increasing stand age in both mineral and biofertilized plots but remained relatively unchanged in controls, indicating that the positive richness response to fertilization was weaker in older stands. Declining understory richness during forest development has previously been associated with canopy closure and reduced light availability (Widenfalk & Weslien 2009; Majasalmi & Rautiainen 2020). One possible

explanation is that fertilization stimulates tree growth and canopy development, thereby accelerating the reduction in understory light availability as stands mature (Jetsonen et al. 2024). Such changes could counteract the positive effects of nutrient enrichment on species richness. However, because canopy cover and light availability were not measured, this mechanism remains hypothetical.

For community composition, fertilization remained significant after accounting for the environmental covariates, explaining 8.05% of Bray–Curtis variation and 5.53% of Jaccard variation. To put that in perspective, the full model explained 39.9% of richness variation through fixed effects and 53.5% when random effects were included. Treatment affected both presence–absence and cover-weighted composition, whereas soil moisture significantly influenced only Bray–Curtis composition and not Jaccard variation. This suggests that soil moisture may primarily influence the relative cover of understory species (measured here as the abundance with Bray-Curtis) rather than consistently determining their presence or absence, measured by Jaccard. However, most compositional variation remained unexplained, indicating that local environmental conditions and other unmeasured factors contributed to differences among communities.

The measured environmental variables were not exhaustive. Soil properties such as pH, C/N ratio and nutrient availability could explain additional variation, given that soil pH can modify vegetation responses to nitrogen enrichment (Hedwall et al. 2021) and fertilization can alter soil nitrogen concentrations and C:N ratios (Jetsonen et al. 2024). Previous management practises and disturbances may also contribute to unexplained variation. Drainage can alter soil biogeochemistry and understory cover (Ågren et al. 2024), while soil preparation can leave detectable effects on understory vegetation for several decades (Hjelm et al. 2025).

The significant interaction found between fertilization and stand age indicates that fertilization-related differences in richness were smaller in older stands. This may reflect either weaker initial responses in stands that were older when fertilization occurred, or changes associated with stand development, potentially involving canopy structure and resource availability. For forest management, this suggests that stand age should be considered when evaluating the potential impacts of mineral and organic fertilization on biodiversity. In conventional Swedish forestry, fertilization is generally applied approximately 10–15 years before final harvesting (From et al. 2015). The long-term effects on species richness observed in this study may differ from those under conventional forest management, as the studied stands remained unharvested for longer than would typically be expected. The weaker richness response observed in older fertilized stands does not necessarily indicate better ecological recovery, since fertilization also altered species composition and reduced the cover of characteristic understory groups. Consequently, assessing the ecological suitability of biofertilization requires consideration of both forest developmental stage and potential changes in

understory community composition, rather than relying solely on species richness. At the landscape scale, these findings suggest that biodiversity outcomes may depend on the proportion and distribution of fertilized stands across age classes. Retaining unfertilized stands could help conserve characteristic understory communities, although landscape-scale effects were not assessed here.

4.6 Broader ecological implications of understory community changes

While species richness was higher under fertilized conditions, the broader ecological implications of the functional changes extend beyond the observed increase in species richness. While some of the impacts of fertilization might be regarded as minor in ecological importance, they should not be overlooked at larger scales. *Vaccinium* species contribute to important boreal ecosystem processes and provide forage for herbivores (Nilsson Hegethorn & Wardle 2005). Spitzer et al. (2021) found that a higher competition for *Vaccinium* species was associated with altered moose (*Alces alces*) feeding patterns, including increased consumption of Scots pine and potential conflicts with forest owners. Bilberry, which was the most abundant dwarf-shrub across all treatments has also been positively associated with early brood survival for black grouse (*Tetrao tetrix*) (Ludwig et al. 2010), while reductions in bilberry biomass decreased the abundance of associated herbivorous insects (Synnøve Lilleeng et al. 2021). Furthermore, bilberry flowers support bumblebees and other pollinators (Bartholomée et al. 2024). Likewise, reduced ground-lichen cover may affect winter forage availability for reindeer and associated husbandry (Kivinen et al. 2010; Sandström et al. 2016). Lichens also provide microhabitats for small invertebrates and influence nutrient cycling (Asplund & Wardle 2017; Roos et al. 2025).

In contrast, increases in forbs and graminoids may benefit other organisms. Flowering forbs such as *Chamaenerion angustifolium*, which increased under organic fertilization, provide nectar for pollinating insects (Pengelly & Cartar 2011), while flower availability influences forest pollinator activity (Diaz-Calafat et al. 2026). More herbaceous vegetation could also increase seasonal forage for some herbivores, as forbs constitute an important component of the moose diet, particularly during summer (Shively et al. 2019). Changes in ericaceous shrub abundance can additionally alter fungal communities, nitrogen availability and litter decomposition (Fanin et al. 2022). Although these responses were not measured in this study, they suggest that fertilization may benefit some ecological groups while disadvantaging others through a modified understory community.

4.7 Limitations

Several aspects of the study design limit the interpretation of these results. Vegetation was surveyed only once, ~20 years after fertilization, and no pre-treatment vegetation data were available, which prevented reconstruction of temporal trajectories. One intermediate measurement (for example 10 years after initial fertilization) could have helped reconstruct the temporal trajectory of understory vegetation responses. However, the fieldwork period was restricted to one season.

In addition, fertilizer type was confounded with nutrient quantity for practical reasons when the stands were fertilized, which means that the differences between mineral and biofertilized stands cannot be attributed to individual components of each treatment type (total nitrogen addition, nutrient release rate or fertilizer composition). Total nitrogen addition was known in advance (Sahlén 2012) but not included as an additional covariate because it was strongly associated with fertilizer type, with no overlap in nitrogen application rates between mineral and biofertilized areas. Including both variables (fertilization type and total nitrogen addition) in the models would have introduced multicollinearity, limiting the reliability and interpretation of their independent effects.

Some covariates had limited spatial precision. Although soil moisture was assessed within a 3 m radius around each plot, the SLU map's 2 x 2 m resolution could not resolve variation within the 0.25 m^2 vegetation plots. Reclassification from the initial 255 soil moisture categories to four categories further simplified locally heterogenous conditions. Distance to open environments was also averaged by treatment area, obstructing plot-level differences. These limitations may have reduced the ability to detect precise relationships with vegetation. Furthermore, several potentially relevant covariates were not measured, including soil chemistry, canopy openness, light availability and basal area, which could have helped clarify the contribution of fertilization on species richness and composition better among stands.

One additional limitation was that lichens were not identified to taxon level, which limited assessment of species-specific responses and may have underestimated richness, particularly in control stands, where lichens were more abundant. Despite these limitations, the study design and analyses provided consistent evidence of differences in understory vegetation among treatments nearly two decades after initial fertilization.

5. Conclusion

This study demonstrates that forest fertilization can leave detectable effects on understory vegetation ~20 years after nutrient addition. Across the 13 sites, fertilization was associated with four main vegetation responses. Firstly, both mineral and biofertilization increased understory species richness, with the highest values under biofertilization. Secondly, fertilization significantly altered community composition, favouring forbs and graminoids while reducing the cover of characteristic dwarf shrubs and ground lichens, although no significant changes in within-area beta diversity were observed. Community-weighted ecological indicators also revealed a shift toward species associated with higher nutrient availability and lower-light conditions, particularly under biofertilization. Finaly, fertilization remained the most consistent predictor of species richness after accounting for environmental covariates.

The higher species richness observed in fertilized areas should not necessarily be interpreted as an overall improvement in biodiversity, since nutrient-associated species increased while characteristic components of nutrient-poor boreal forest floors, such as dwarf shrubs and lichens, declined. Biofertilization with the sewage-sludge-derived product Bionäring generally produced stronger long-term responses in understory vegetation than conventional mineral fertilization. However, these differences cannot be attributed solely to fertilizer type, as the treatments differed in nutrient input and composition. Although fertilization could increase landscape-level variation by creating difference between treated and untreated stands, widespread application could reduce the extent of characteristic nutrient-poor communities. Higher variation would therefore not necessarily imply conservation benefits.

Forest fertilization contributes to increased tree growth and carbon uptake, but these benefits must also be weighed against changes in understory vegetation and other ecosystem processes. Whether mineral or organic fertilization represents a sustainable management practice depends not only on forest productivity but also on the ecological characteristics and conservation objectives of the treated stands. Although repeated fertilization has been investigated, knowledge of its cumulative effects on the understory vegetation, microbial communities and nutrient cycling across successive forest rotations remains limited. Understanding these uncertainties is particularly important given the growing interest in forest fertilization as a climate mitigation strategy (Jämtgård et al. 2026). Long-term monitoring across forest rotations, including soil nutrients, canopy structure and understory light, could clarify vegetation responses, cumulative effects and conditions that minimize the ecological impacts of fertilization.

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Popular science summary

Fertilizing forests can increase tree growth and timber production. In the nutrient-poor boreal forests of northern Fennoscandia, tree growth is often limited by the availability of nitrogen, making fertilization an effective way to increase forest productivity. However, the forest ecosystem consists of much more than only trees and timber. The understory vegetation, including dwarf shrubs, grasses, herbs, mosses and lichens, is an important part of the ecosystem. Changes to this vegetation can have negative consequences for biodiversity and other ecological functions.

This study investigated whether forest fertilization still affected understory vegetation 18-20 years after fertilizers were initially applied. Thirteen forest stands in Norrbotten were surveyed. Within each site, three areas were compared: one fertilized with conventional mineral fertilizer, one fertilized with an organic fertilizer produced from treated sewage sludge, and one that had not been fertilized. The fertilizers were first applied between 2006 and 2008, with mineral-fertilized areas receiving a second application three years later. During the summer of 2026, vegetation was surveyed in a total of 975 plots measuring 50 × 50 cm, where the cover of each plant and moss species present within the grid was recorded, together with ground lichen cover.

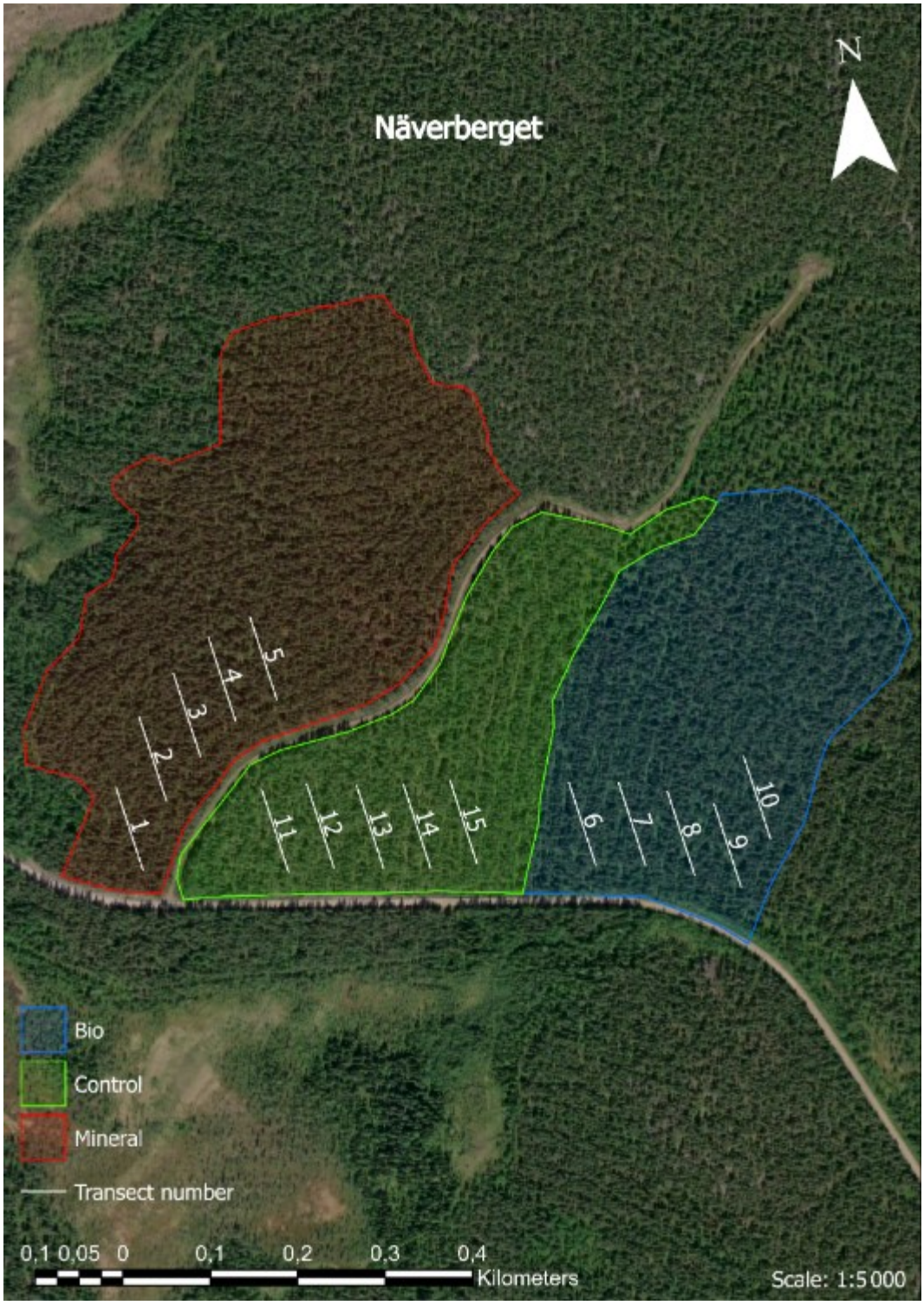
The results showed that differences in ground vegetation were still measurable 18-20 years after the initial fertilization. Forest areas that had been fertilized contained more understory plant species. On average, 7.3 species were found in each vegetation plot (0.25 m2) in control areas, compared to 8.6 after mineral fertilization and 9.3 after organic fertilization. When all plots within each treatment area were considered together, the same pattern was observed, with the highest number of species occurring in organically fertilized areas. However, the type of vegetation was also altered. Fertilized areas contained more grasses and herbs, while dwarf shrubs declined. Several plant species associated with more nutrient-rich conditions became more widespread, especially in organically fertilized stands. At the same time, lingonberry (*Vaccinium vitis-idaea*), a characteristic dwarf shrub of Fennoscandian boreal forests, declined. Fertilized areas contained more species typically associated with nutrient-rich and shaded forest environments, although soil nutrients and light availability were not directly measured. Ground lichens also showed a negative response to fertilization, with lower cover in both fertilization treatments, and a lower occurrence following organic fertilization. Such changes are particularly relevant in northern Sweden, where ground lichens are an important source of winter forage for reindeer.

Organic fertilization often produced the strongest responses, but this does not necessarily mean that the type of fertilizer alone caused the difference. The organic and mineral treatments differed in the total amount of nitrogen applied, their

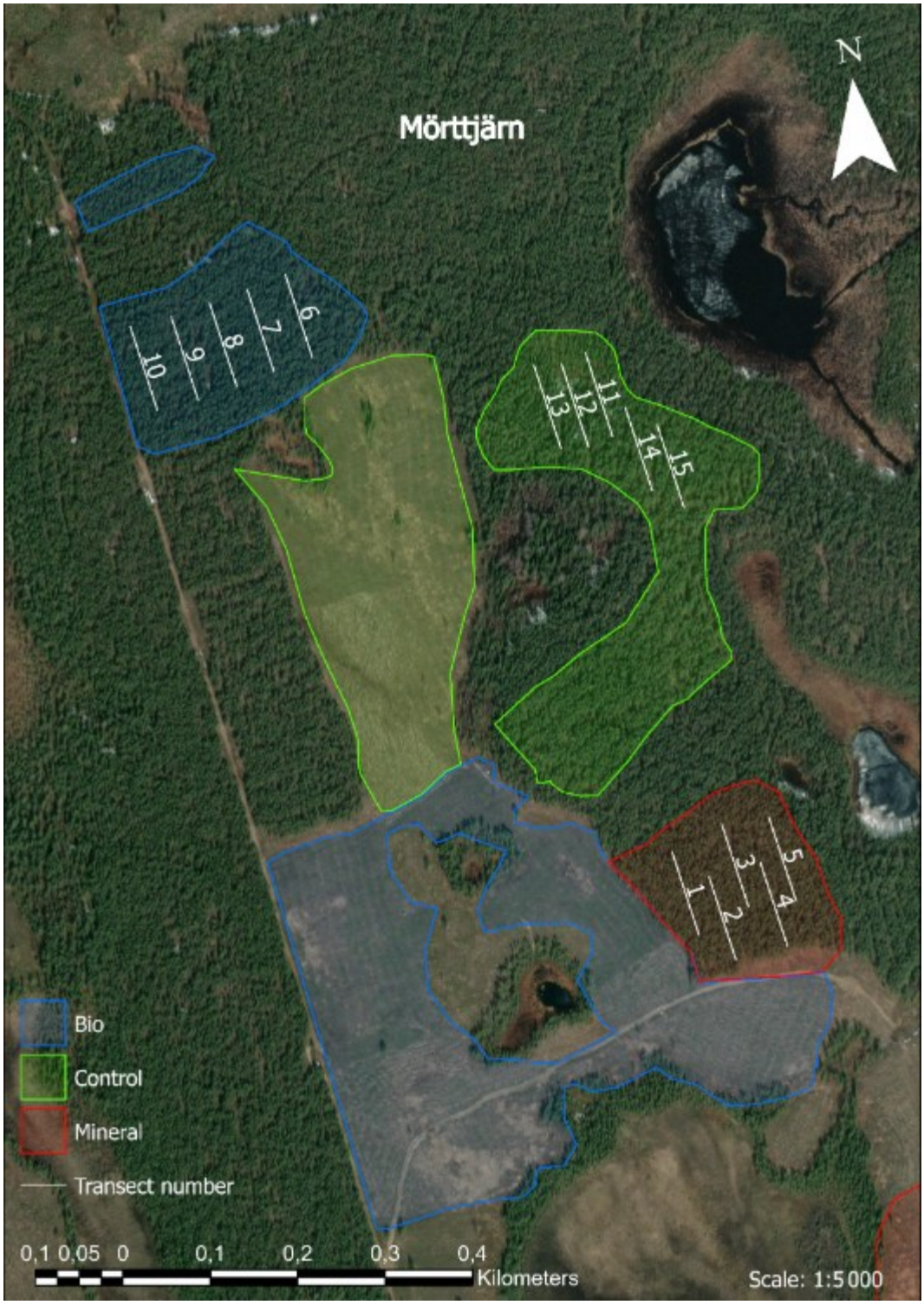
composition, and the rate at which nutrients became available to vegetation. These differences make it difficult to separate the effect of fertilizer type from the effect of nutrient input alone. Forest age, soil moisture and dominant tree species also helped explain differences in ground vegetation, but fertilization remained an important factor even after accounting for these environmental conditions. Furthermore, because vegetation was surveyed only once and no measurements were available from before fertilization, the study could not determine how the vegetation had changed over a temporal trajectory. Nevertheless, the results showed that both conventional and organic fertilizers can be associated with long-term changes in understory vegetation.

The results show that increasing forest productivity may come at the expense of characteristic ground vegetation, even when overall, the species richness increases. Although fertilization can enhance tree growth and carbon uptake, these benefits must be weighed against its long-term effects on understory vegetation and the wider ecosystem. Fertilization decisions should therefore consider not only forest productivity but also the existing vegetation, particularly in stands where shrubs and lichens have ecological or conservation importance.

Appendix 1 – Map of Näverberget



Appendix 2 – Map of Mörttjärn



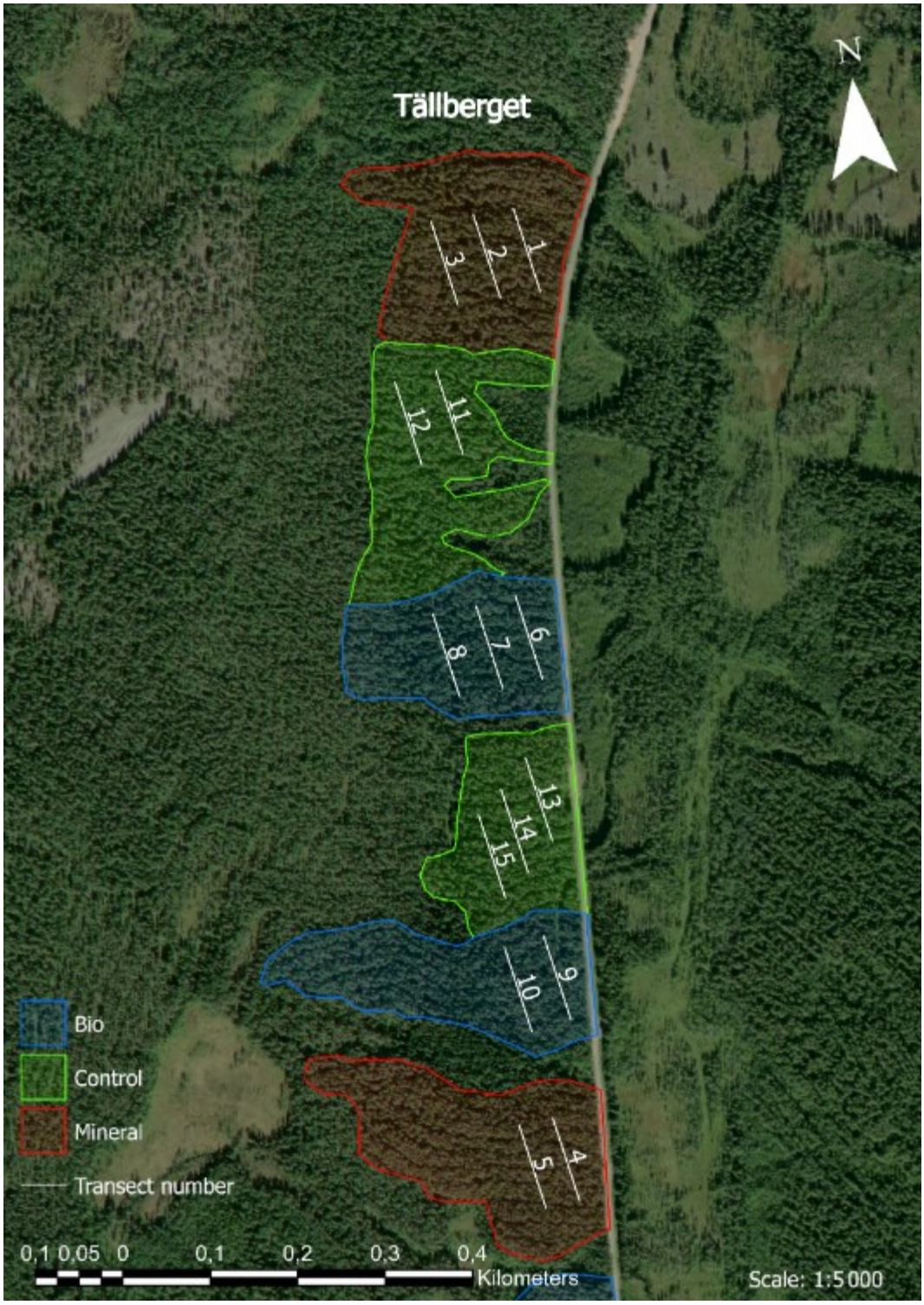
Appendix 3 – Map of Hällberget



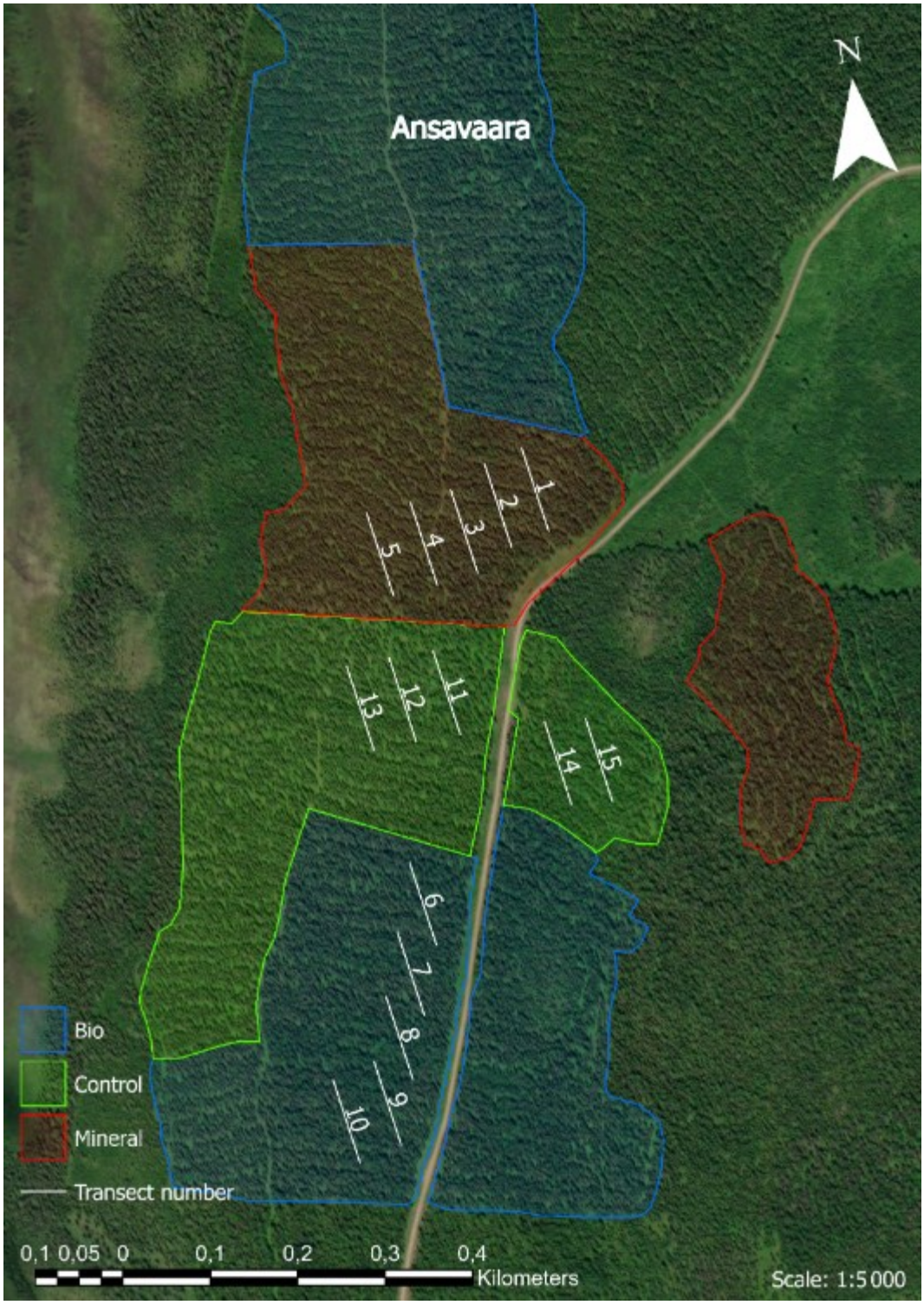
Appendix 4 – Map of Lillfuruberget



Appendix 5 – Map of Tällberget



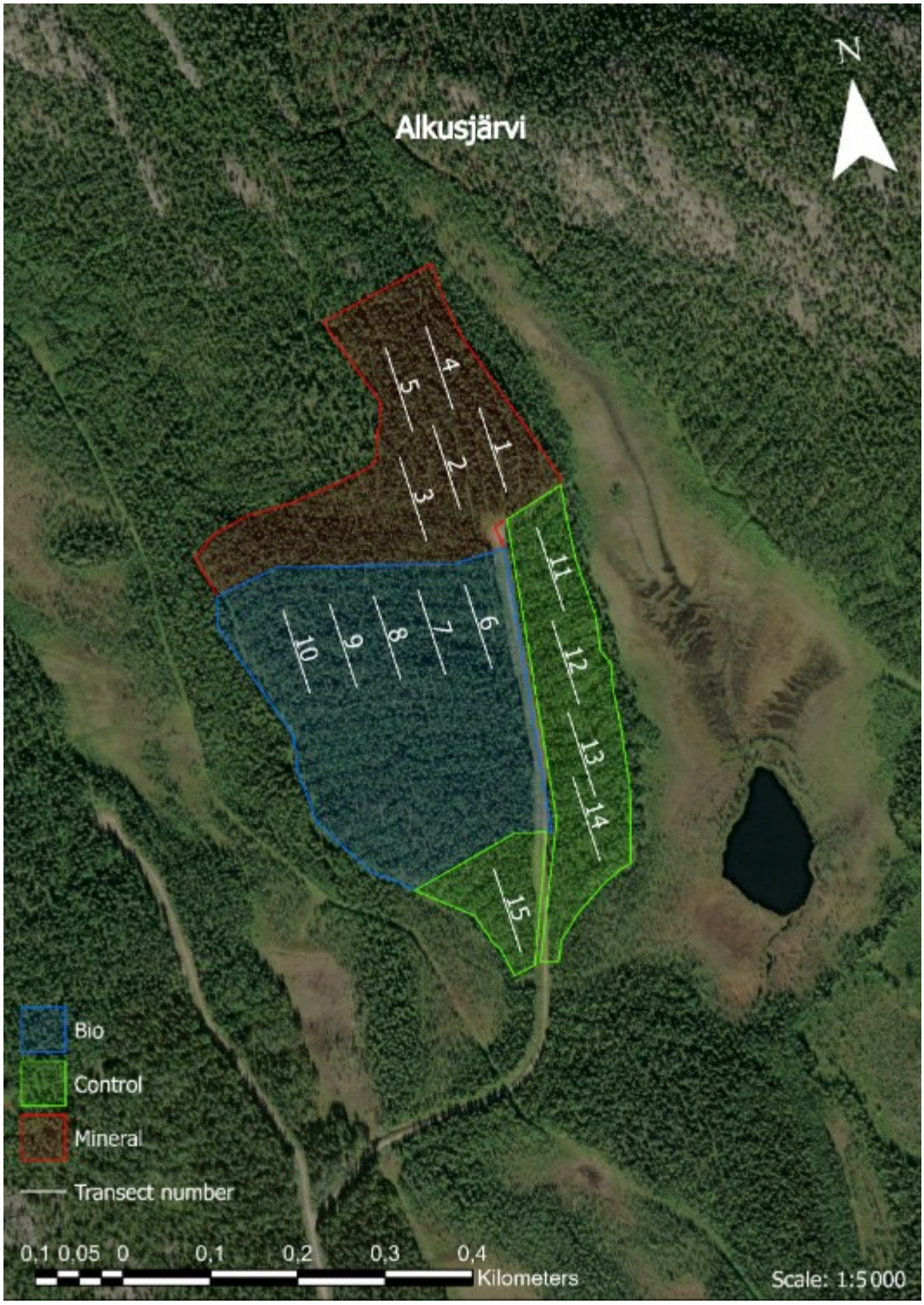
Appendix 6 – Map of Ansavaara



Appendix 7 – Map of Peuravaara



Appendix 8 – Map of Alkusjärvi



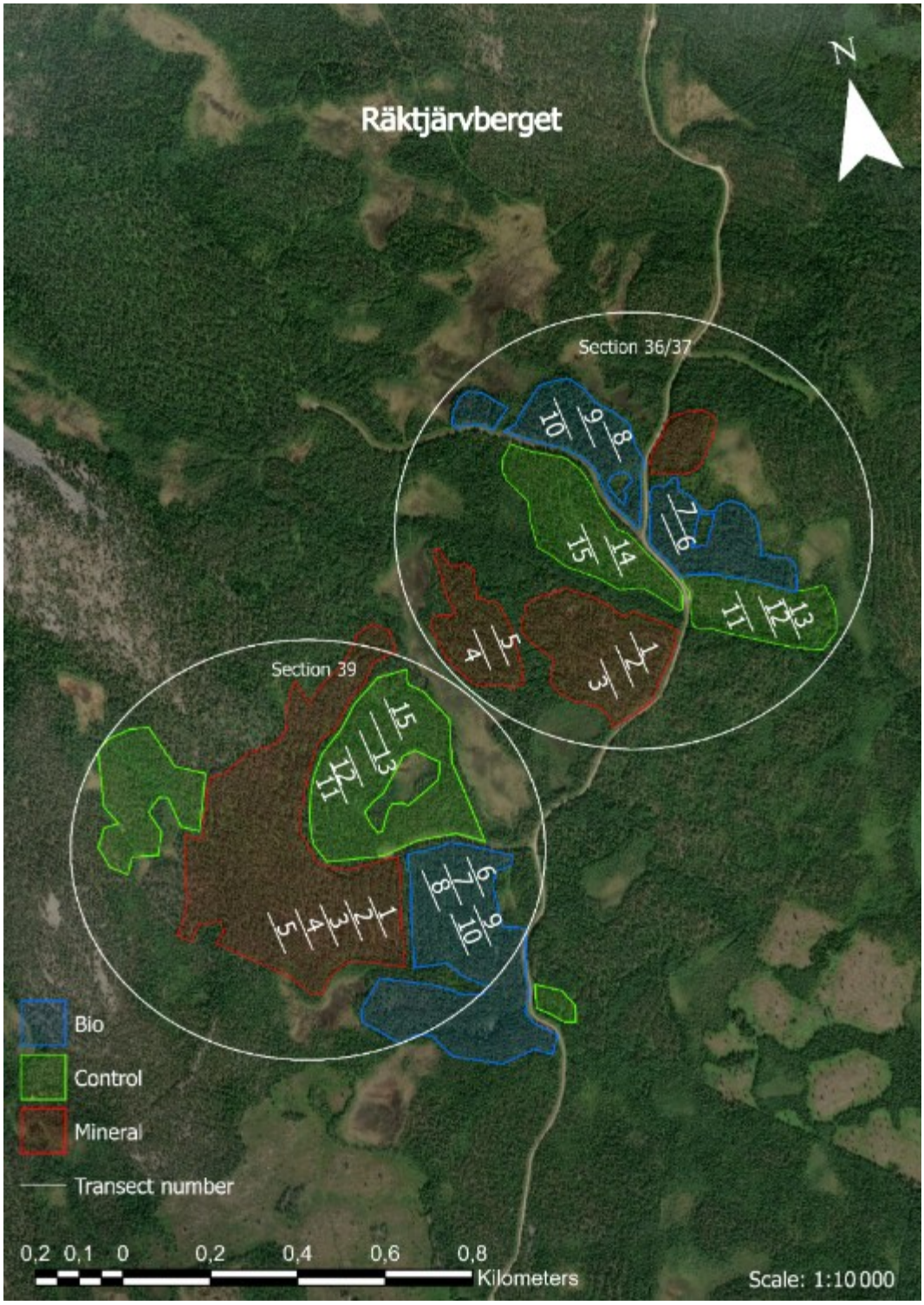
Appendix 9 – Map of Hautamaa



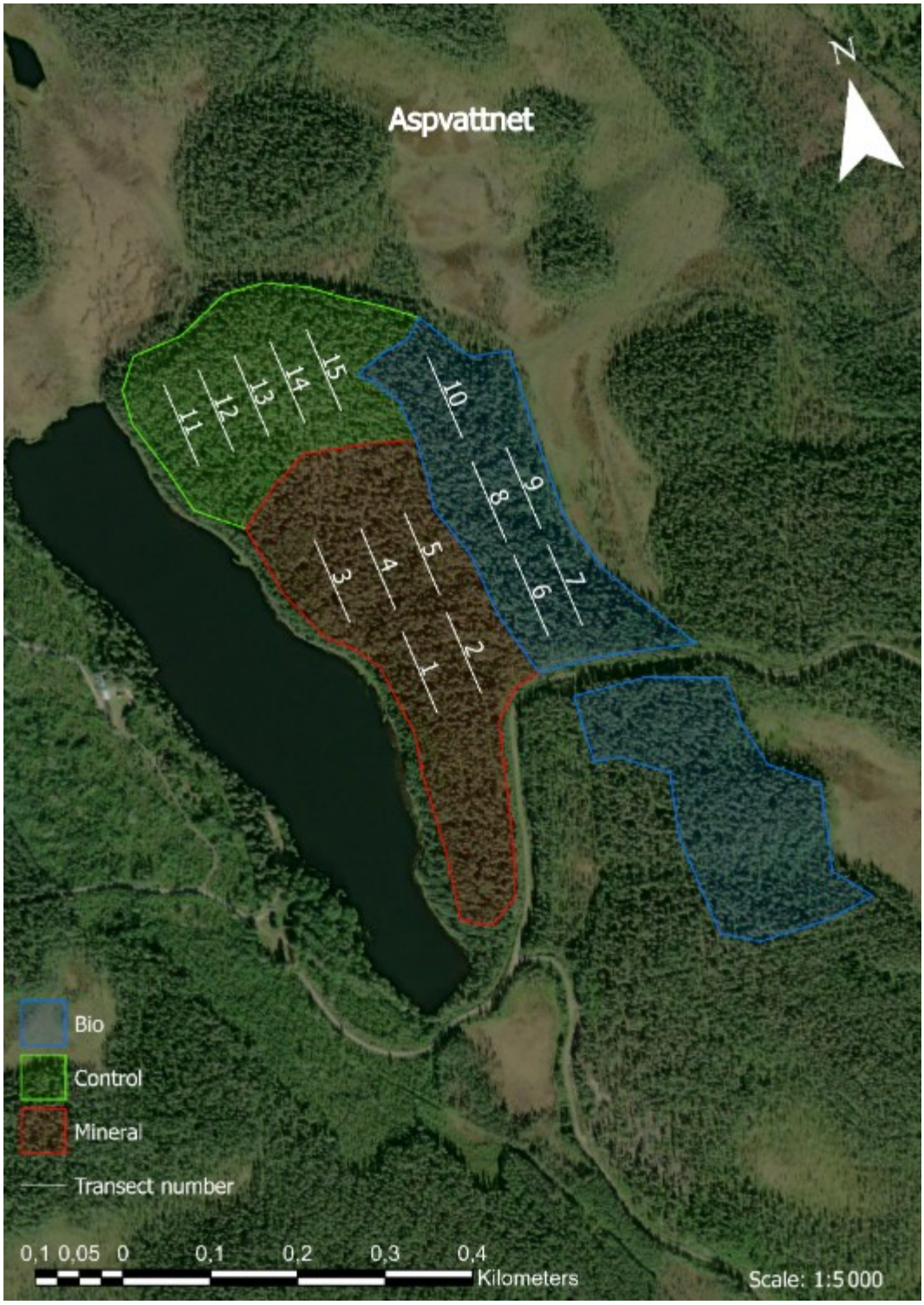
Appendix 10 – Map of Vittakero



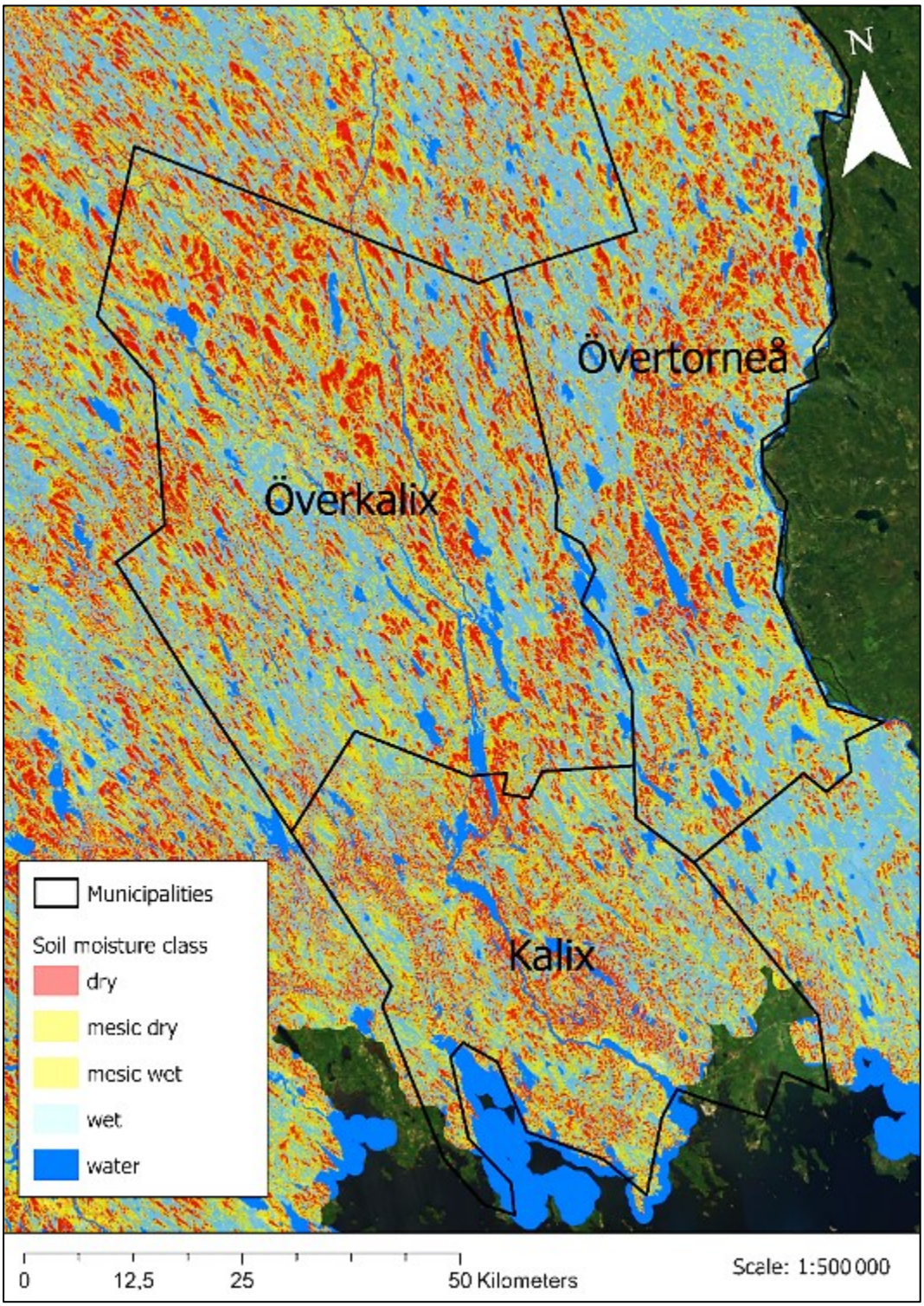
Appendix 11 – Map of Räktjärvberget



Appendix 12 – Map of Aspvattnet



Appendix 13 – Soil moisture map



Appendix 14 – Study design in practice



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Plot in the control stand in Näverberget

- One full square is equal to 4% of the total cover (4% × 25 = 100%).
- Estimated ground lichen cover: 22%
- *Calluna vulgaris*: 8%
- *Dicranum scoparium*: 2%
- *Pleurozium schreberi*: 3%
- *Polytrichum juniperum*: 4%
- *Vaccinium vitis-idaea*: 15%

Appendix 15a – Mean species cover across treatments 1/4

Species	Mineral	Bio	Control
Alaucomium palustre	0.18	0.17	0.06
Andromeda polifolia	0.00	0.00	<0.01
Angelica sylvestris	ND	ND	ND
Antennaria dioica	ND	ND	ND
Arctostaphyllos uva-ursi	0.00	0.04	0.00
Athyrium filix-femina	0.02	0.00	0.00
Avenella flexusoa	7.37	7.41	1.78
Barbilophozia barbata	0.21	0.11	0.02
Barbilophozia lycopodioides	0.64	0.57	0.12
Brachypodium sylvaticum	0.03	0.00	0.10
Brachytecium rutabulum	ND	ND	ND
Brachytecium salebrosum	0.59	0.96	0.38
Calamagrostis arundinacea	ND	ND	ND
Calliergon cordifolium	<0.01	0.00	<0.01
Calluna vulgaris	0.98	0.95	0.78
Calypogeia integristipula	0.00	<0.01	0.00
Carex echinata	ND	ND	ND
Carex globularis	0.10	0.54	0.36
Carex magellanica	ND	ND	ND
Chamaenerion angustifolium	0.09	0.78	0.03
Chiloscyphus pallescens	<0.01	0.00	0.00
Cicerbita alpina	ND	ND	ND
Cirsium heterophyllum	0.00	0.14	0.00
Comarum palustre	ND	ND	ND
Convallaria majalis	0.05	0.02	0.02
Cornus suecica	0.33	1.33	0.22
Dactylorhiza fushii	ND	ND	ND

ND = species observed within the study sites/treatment areas but not detected within the vegetation sampling plots.

Appendix 15b – Mean species cover across treatments 2/4

Species	Mineral	Bio	Control
Dactylorhiza maculata	<0.01	0.02	<0.01
Dicranum montanum	ND	ND	ND
Dicranum polysetum	7.30	6.56	6.88
Dicranum scoparium	0.04	<0.01	0.39
Diphasiastrum complanatum	0.04	0.03	0.00
Dryopteris carthsiana	0.18	0.28	0.00
Dryopteris expansa	ND	ND	ND
Empetrum nigrum	1.64	1.19	3.58
Equisetum sylvaticum	0.61	1.77	0.50
Festuca rubra	0.00	<0.01	0.02
Filipendula ulmaria	ND	ND	ND
Fumaria officinalis	0.00	<0.01	0.00
Geranium sylvaticum	0.48	0.53	0.14
Goodyera repens	ND	ND	ND
Gymnocarpium dryopteris	4.26	9.24	2.23
Hieracium murorum	0.02	0.03	0.00
Hylocomiadelphus triquetrus	0.18	0.28	0.05
Hylocomium splendens	9.98	7.23	11.37
Juncus filiformis	0.00	0.01	0.00
Juniperus communis	0.04	0.11	0.25
Linnea borealis	2.95	4.29	2.00
Lophocolea heterophylla	<0.01	<0.01	0.00
Luzula pilosa	1.32	1.67	0.23
Lycopodium clavatum	0.00	0.00	0.02
Lysimachia europaea	1.64	1.99	1.17
Maianthemum bifolium	3.80	4.44	1.76
Matricharia polymorpha	ND	ND	ND

ND = species observed within the study sites/treatment areas but not detected within the vegetation sampling plots.

Appendix 15c – Mean species cover across treatments 3/4

Species	Mineral	Bio	Control
Melampyrum sylvaticum	1.11	1.65	0.72
Melica nutans	0.32	0.04	0.01
Milium effusum	0.00	0.18	0.00
Monses uniflora	ND	ND	ND
Orthilia secunda	0.11	0.41	0.15
Paris quadrifolia	ND	ND	ND
Pellia neesiana	ND	ND	ND
Phegopteris connectillis	0.13	0.37	0.10
Plagiomnium ellipticum	0.08	0.17	0.02
Plagiothecium denticulatum	0.00	0.04	0.00
Platanthera bifolia	ND	ND	ND
Pleurozium schreberi	20.68	17.95	26.76
Poa nemoralis	0.60	1.03	0.20
Poa trivialis	0.54	0.50	0.10
Pohila nutans	0.25	0.35	0.05
Polytrichum commune	3.16	5.82	1.89
Polytrichum juniperum	0.00	0.03	0.15
Polytrichum strictum	0.21	0.00	0.00
Ptilidium ciliare	0.02	0.00	0.19
Ptilium crista castrensis	0.92	0.12	0.07
Ptilium pulcherrimum	0.09	0.00	0.05
Pyrola chlorantha	ND	ND	ND
Pyrola minor	0.02	0.14	0.00
Pyrola rotundifolia	0.00	0.02	<0.01
Racomitrium fasciculare	0.04	0.00	0.07
Ranunculus acris	ND	ND	ND
Rhizomnium punctatum	<0.01	0.02	<0.01

ND = species observed within the study sites/treatment areas but not detected within the vegetation sampling plots.

Appendix 15d – Mean species cover across treatments 4/4

Species	Mineral	Bio	Control
Rhodobryum roseum	0.02	0.03	0.00
Rhododendron tomentosum	0.57	0.72	0.72
Rubus chamaemorum	0.00	0.02	0.06
Rubus idaeus	0.00	0.13	0.00
Rubus saxatilis	0.50	0.27	0.10
Silene dioica	ND	ND	ND
Solidago virgaurea	1.93	2.59	0.84
Sphagnum capillifolium	0.66	0.24	0.70
Sphagnum fimbriatum	0.14	0.08	0.00
Sphagnum girgensohnii	0.97	1.69	1.29
Sphagnum riparium	0.09	0.06	0.00
Sphagnum squarrosum	0.00	0.02	<0.01
Sphagnum warnstorfii	0.00	0.00	<0.01
Sphagnum wulfianum	0.00	0.03	0.00
Spinulum annotinum	0.54	0.55	0.89
Stellaria graminea	ND	ND	ND
Straminergon stramineum	0.02	<0.01	0.00
Vaccinium microcarpium	0.03	0.03	0.05
Vaccinium myrtillus	32.65	31.89	43.94
Vaccinium oxycoccos	0.06	0.02	<0.01
Vaccinium uliginosum	1.11	0.68	2.93
Vaccinium vitis-idaea	7.66	5.66	13.06
Viola palustris	0.00	0.10	0.00

ND = species observed within the study sites/treatment areas but not detected within the vegetation sampling plots.

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2026:10 Författare: Xinyao Shang
Effects of Nitrogen Fertilization, Water Treatment, and Environment on Nitrogen Fixation in Boreal Forest Species

2026:11 Författare: Yue Wu
Linking root trait with wood density and vitality of Scots pine breeds (Pinus sylvestris)

2026:12 Författare: Matthew Coker
Decadal patterns of tree regeneration following wildfire
Effects of fire severity in boreal forests of central Sweden

2026:13 Författare: Axel Manngård
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2026:14 Författare: Julia Wikström
Does Downed Deadwood Influence Ungulate Browsing Pressure in Forest Regeneration: A Systematic Literature Review

2026:15 Författare: Fredrik Bergman
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Flottningen i Indalsälven – från etablering till avveckling

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