Petteri Kiilunen is a physical geographer whose research lies at the intersection of plant ecology, macroecology, and biogeography. He is interested in long-term changes in plant communities across boreal and tundra environments, with the aim of understanding how vegetation and biodiversity change across space and time. In his doctoral thesis, Kiilunen examines long-term vegetation changes across Northern Fennoscandia using vegetation resurvey data and a systematic literature review. The thesis reveals substantial but ecosystem-specific vegetation changes and emphasizes the importance of regional perspectives for understanding ecological responses to global change. Through his work, Kiilunen contributes to a broader understanding of long-term ecosystem dynamics in a rapidly changing world.

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# High-latitude vegetation shifts in the era of global change: Multi-decade ecosystem-level evidence from Northern Europe

Petteri Kiilunen

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# High-latitude vegetation shifts in the era of global change: Multi-decade ecosystem-level evidence from Northern Europe

Petteri Kiilunen

Academic dissertation to be presented with the permission of the Doctoral Training Committee for Technology and Natural Sciences of the University of Oulu Graduate School (UniOGS) for public discussion in the lecture hall L6 on the 16th of October 2026 at 12.

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## Abstract

Biodiversity is increasingly threatened by human-induced global change drivers that restructure ecosystems. High-latitude ecosystems are particularly vulnerable to climate change, which alters vegetation composition, diversity, and functioning. However, long-term vegetation change has not progressed uniformly across circumpolar and boreal regions. This thesis focuses on one such region, Northern Fennoscandia, which lies in a transition zone between boreal forests and Arctic tundra in Northern Europe. The thesis examines decadal-scale vegetation changes using observational plant community data, synthesizes existing evidence of long-term vegetation changes across the region, and compares whether the observed changes align with or diverge from the wider circumpolar and boreal trends. By combining empirical resurvey studies with a systematic literature review, the thesis provides a broad region-wide perspective on diverse long-term vegetation changes across northern ecosystems.

First, the thesis examines long-term changes in the composition and diversity of plant communities in heathlands and tundra (Study I). Second, it analyzes changes in the prevalence of pollinator dependence and pollen and nectar provision of vascular plant communities across heathlands and tundra and boreal herb-rich forests (Study II). Third, long-term vegetation changes across Northern Fennoscandia's four main terrestrial ecosystems (heathlands and tundra, mountain birch forests, boreal forests, and peatlands) are summarized via a systematic literature review (Study III).

The results showed that the heathlands and tundra of Northern Fennoscandia have undergone biotic homogenization over decades resulting from changed local patterns of dominant species. These changes are linked to the shrubification of tundra communities driven primarily by the evergreen crowberry (*Empetrum nigrum*). Despite otherwise being consistent with circumpolar evidence, shrubification in Northern Fennoscandia is not driven by deciduous shrubs. The prevalence of both pollinator dependence and pollen and nectar provision has decreased in heathlands and tundra, and in boreal herb-rich forests, underscoring the links between vegetation change and ecosystem functioning. The systematic literature review further revealed that several vegetation changes commonly observed across circumpolar and boreal regions remain ambiguous in Northern Fennoscandia. The review found no evidence of widespread or distinct borealization, thermophilization, or altitudinal shifts in heathland and tundra plant communities, although signs of these processes are emerging. Forests have become denser, but tree and forest lines have not advanced uniformly. Peatland vegetation change remains critically understudied due to the scarcity of long-term repeated sampling studies.

The thesis concludes by recommending that future studies should more explicitly account for key environmental gradients and spatial scale to better capture and resolve the heterogeneity that arises from locally varying vegetation responses. Continued long-term, field-based monitoring is essential. A critical next step would be to advance the understanding of how long-term vegetation changes have affected ecosystem functioning in Northern Fennoscandia because they impact the livelihoods of indigenous communities and efforts to mitigate climate change and its global impacts.

**Keywords:** boreal forests, *Empetrum nigrum*, heathlands and tundra, long-term vegetation change, Northern Fennoscandia, plant communities, shrubification

## Tiivistelmä

Ihmisen aiheuttama globaalimuutos uhkaa luonnon monimuotoisuutta. Pohjoisten alueiden ekosysteemit ja niiden kasvillisuus ovat erityisen alttiita ilmastonmuutoksen vaikutuksille. Kasvillisuuden pitkän aikavälin muutokset eivät kuitenkaan ole edenneet yhtenäisesti eri sirkumpolaarilla ja boreaalisilla alueilla. Tämä väitöskirja keskittyy yhteen näistä alueista, Pohjois-Fennoskandiaan, joka sijaitsee boreaalisten metsien ja arktisen tundran vaihettumisvyöhykkeellä Pohjois-Euroopassa. Väitöskirja tarkastelee vuosikymmenten mittakaavassa tapahtuvia kasvillisuusmuutoksia hyödyntäen kasviyhteisöaineistoja, muodostaa synteesin muissa tutkimuksissa havaituista kasvillisuusmuutoksista alueella sekä vertailee, noudattavatko alueella havaitut muutokset sirkumpolaarisella mittakaavalla havaittuja muutostrendejä vai poikkeavatko ne niistä. Yhdistämällä empiiriset uudelleenkartoitustutkimukset systemaattiseen kirjallisuuskatsaukseen väitöskirja tarjoaa laajan alueellisen näkökulman pohjoisten ekosysteemien moninaisiin pitkäaikaisiin kasvillisuusmuutoksiin.

Väitöskirja tarkastelee ensimmäiseksi pitkän aikavälin muutoksia kasviyhteisöjen koostumuksessa ja monimuotoisuudessa puuttomilla merenrantanummilla ja tunturikankailla (Study I). Toiseksi se analysoi muutoksia putkilokasviyhteisöjen pölytysriippuvuudessa ja siitepölyn- ja medentuotannossa merenrantanummilla ja tunturikankailla sekä boreaalisissa lehtometsissä (Study II). Kolmanneksi Pohjois-Fennoskandian neljän yleisimmän maaekosysteemin (nummet ja tunturikankaat, tunturikoivikot, boreaaliset metsät ja suot) pitkäaikaiset kasvillisuusmuutokset kootaan yhteen systemaattisen kirjallisuuskatsauksen avulla (Study III).

Väitöskirjan tulokset näyttivät, että Pohjois-Fennoskandian nummien ja tundran kasviyhteisöissä on tapahtunut samankaltaistumista eli bioottista homogenisaatiota, joka on seurausta valtalajeissa tapahtuneista paikallistason muutoksista. Nämä muutokset liittyvät erityisesti ainavihannan varvun, variksenmarjan (*Empetrum nigrum*) merkittävään lisääntymiseen alueella. Vaikka ilmiö noudattelee sirkumpolaarisella skaalalla havaittua pensastumistrendiä, Pohjois-Fennoskandiassa se ei ilmene kausivihantien pensaiden ja varpujen lisääntymisenä. Putkilokasvien pölytysriippuvuus ja siitepölyn- ja medentuotanto ovat aiempaa vähäisempiä sekä nummilla ja tunturikankailla että lehtometsissä, mikä korostaa yhteyttä kasvillisuuden ja ekosysteemitoimintojen muutosten välillä. Systemaattinen katsaus osoitti, että useimpia sirkumpolaarisella skaalalla raportoituja kasvillisuusmuutoksia ei ole havaittu Pohjois-Fennoskandiassa. Katsauksessa ei havaittu laajaa nummi- ja tunturiyhteisöjen borealisaatiota, termofilisaatiota tai levinneisyysmuutoksia, vaikka paikoin havaittiin varhaisia merkkejä näistä muutoksista. Metsien kohdalla havaittiin kasvillisuuden tihentymistä. Suokasvillisuuden pitkäaikaismuutostutkimuksen havaittiin olevan puutteellista. Väitöskirjan lopuksi suositellaan, että tulevissa tutkimuksissa tulisi ottaa entistä selkeämmin huomioon keskeiset ympäristögradientit ja alueellinen mittakaava, jotta kasvillisuusmuutosten paikallisesta vaihtelusta johtuva tulosten heterogeenisyys voitaisiin paremmin havaita ja ratkaista. Kenttähavaintoihin perustuvaa pitkäaikaisseurantaa on jatkettava tulevaisuudessa. Tärkeä seuraava askel on edistää tutkimusta, joka tarkastelee kasvillisuusmuutosten vaikutuksia useisiin eri ekosysteemitoimintoihin Pohjois-Fennoskandiassa, sillä ne vaikuttavat muun muassa alkuperäiskansojen elinoloihin ja yrityksiin hillitä ilmastonmuutosta ja sen globaaleja seurauksia.

**Avainsanat:** boreaaliset metsät, *Empetrum nigrum*, nummet ja tundra, pitkäaikaiset kasvillisuusmuutokset, Pohjois-Fennoskandia, kasviyhteisöt, pensastuminen

## List of original publications

This thesis is based on the following publications, which are referred to throughout the text by their Roman numerals:

Study I Maliniemi T, Kiilunen P, Bråthen KA, Kapfer J, Bockelie Rosendal T, Grytnes JA, Saccone P & Virtanen R (2025) Long-term homogenization of Fennoscandian heathland and tundra vegetation is connected to the expansion of an allelopathic dwarf shrub. *Ecography* 2025: e07921. https://doi.org/10.1002/ecog.07921

Study II Kiilunen P, Maliniemi T, Alahuhta J, Grytnes JA, Virtanen R, Bråthen KA, Happonen K, Kapfer J, Muurinen L, Skalska-Tuomi MW & Ala-Hulkko T (2025) Decades of change in vascular plant composition in high-latitude ecosystems: shifting prevalence of pollination strategies. *Ecology and Evolution* 15(10): e72288. https://doi.org/10.1002/ece3.72288

Study III Kiilunen P, Määttänen AM, Ala-Hulkko T & Maliniemi T (submitted manuscript) Vegetation shifts in Northern Fennoscandia – a systematic review based on contemporary long-term evidence from repeated sampling.

Study I is reprinted under the Creative Commons CC BY 3.0 license, and Study II under the Creative Commons CC BY 4.0 license. Study III is included as the author's submitted manuscript.

## Author's contributions

Study I The research idea was conceptualized by TM and RV, with the support of PK. The data were collected by TM, KAB, JK, TBR, and RV. PK and TM analyzed the data. PK and TM wrote the original manuscript with contributions from all authors.

Study II PK conceptualized the research idea with TM, JA, and TAH. The data were collected by TM, RV, KAB, KH, JK, LM, and MWST. PK analyzed the data with contributions from TM and KH. PK wrote the original manuscript with contributions from all authors.

Study III PK conceptualized the research idea with TM. The literature review was conducted by PK, AMM, TAH and TM. PK led the data curation, analysis, and visualization of the reviewed literature, with support from all co-authors. PK wrote the original manuscript with contributions from all authors.

PK=Petteri Kiilunen, AMM=Aino-Maija Määttänen, JA=Janne Alahuhta, JK=Jutta Kapfer, KAB=Kari Anne Bråthen, KH=Konsta Happonen, LM=Lauralotta Muurinen, MWST=Maria W. Skalska-Tuomi, RV=Risto Virtanen, TAH=Terhi Ala-Hulkko, TBR=Torunn Bockelie Rosendal, TM=Tuija Maliniemi

I used generative AI technology for language editing and for assistance with R coding related to data visualization. I take full responsibility for the content of this dissertation.

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# 1 Introduction

Global change alters biodiversity across the globe by impacting species numbers and abundances (Dornelas et al. 2014; Franklin et al. 2016; IPBES 2019; Pinsky et al. 2025; Vellend et al. 2013, 2017). Some species thrive as they adapt better to change, while others decline. The resulting gains and losses alter community composition. However, disentangling the mechanisms that underlie these shifts is often challenging, owing to the complex interplay of abiotic and biotic processes and their dependence on geographical scale (e.g., Chase et al. 2018, 2019). Currently, researchers and environmental practitioners most often rely on simple, unidimensional biodiversity metrics to quantify biodiversity change, yet these measurements rarely reveal consistent large-scale trends or capture more complex changes in species composition (e.g., Blowes et al. 2019; Dornelas et al. 2023; see also Purvis & Hector 2000). To understand multifaceted biodiversity change and its impact on ecosystem functioning in a changing world (e.g., Cardinale et al. 2012), we need to examine biodiversity from multiple perspectives with a deeper focus on biogeographical variation in species composition and their responses to environmental drivers.

Across the circumpolar north, the impacts of global change on high-latitude ecosystems are driven primarily by climate change (Bowler et al. 2020; Fisher et al. 2019; Franklin et al. 2016; Frost et al. 2025). These ecosystems are under immense pressure as climate change rapidly progresses (Rantanen et al. 2022) and extreme weather events become more frequent (Aalto et al. 2026). Changing conditions impact both the structure and function of plant and animal communities (Bjorkman et al. 2018; Vowles & Björk 2019; see also Aronsson et al. 2021; Taylor et al. 2020), and especially high-latitude vegetation shows strong changes across the main ecosystems from boreal forests to tundra and peatlands (e.g., Aronsson et al. 2021; Berner & Goetz 2022; Bjorkman et al. 2020; Kuuluvainen et al. 2017; Leppiniemi et al. 2023).

Along with changes in temperatures, precipitation, and snow conditions (Post et al. 2009), interactions among plants (García Criado et al. 2025b), herbivores (Kaarlejärvi et al. 2017), and microbes (Classen et al. 2015) are key drivers behind high-latitude vegetation change. Thus, changes in biodiversity are likely to be complex (García Criado et al. 2025b) and may exhibit a delayed emergence (Pacheco-Riaño et al. 2024), thereby requiring a long-term perspective to observe how these ecosystems change over time.

During the 21st century, we have already witnessed numerous impacts of climate change on vegetation (e.g., Bjorkman et al. 2018, 2020; Mekonnen et al. 2021; Rees et al. 2020). These impacts include many interrelated phenomena, such as increased productivity, referred to as arctic greening (Berner et al. 2020) but also decrease of productivity or arctic browning (Berner & Goetz 2022; Myers-Smith et al. 2020), increasing shrub abundance or shrubification (Mekonnen et al. 2021; Myers-Smith et al. 2011, 2015), the expansion of boreal species and communities into treeless tundra or borealization (García Criado et al. 2025b; Verdonen et al. 2026), the replacement of cold-adapted species with warm-adapted species or thermophilization (Elmendorf et al. 2015), and the northward and upward advance of tree and forest lines (Berner & Goetz 2022; Feng et al. 2026; Rees et al. 2020). These phenomena shape the taxonomic (Bjorkman et al. 2020; Bråthen et al. 2024) and functional composition (Davrinche et al. 2026; Everest et al. 2026; Mäkinen et al. 2025) of plant communities and can lead to the decline and eventual loss of arctic species (Pearson et al. 2014). Indeed, future predictions highlight northward distribution shifts of boreal forest species (Pearson et al. 2013; Villén-Peréz et al. 2020), increasing functional similarity among communities,

and a shift toward taller and faster-growing plants in tundra (Niittynen et al. 2020b) along with redistribution (Pearson et al. 2013), homogenization (Stewart et al. 2018), and regional loss (Lagergren et al. 2024) of tundra species and habitat types. Such major changes in plant form, function, and diversity may lead to the transformation of cold-adapted ecosystems toward boreal ecosystems with a decline of tundra species and altered ecosystem functioning, thereby reducing their capacity to maintain essential functions (Hautier et al. 2018; Isbell et al. 2011).

Despite significant progress in understanding global change-driven vegetation changes, evidence remains biased or lacking at many temporal and spatial scales (e.g., Metcalfe et al. 2018; Virkkala et al. 2019). However, as underlying environmental conditions, species composition, and the rate of global changes differ among circumpolar and boreal regions, vegetation trends likely manifest differently across scales (e.g., Bjorkman et al. 2020; Mekonnen et al. 2021). This thesis provides a regional synthesis of the current state of vegetation and past vegetation changes in the high-latitude region of Northern Fennoscandia. This is achieved by combining new insights from rare long-term plant community data with evidence synthesized from previous studies of long-term vegetation changes in the region.

## 2 High-latitude vegetation change: long-term data and regional context

### 2.1 Plant communities under global change

Species are assembled into distinct communities across space and time (Götzenberger et al. 2012). They differ in terms of species identity (which species are present), species numbers (how many species are present, i.e., species richness), and species abundance distribution (how abundant different species are). Plant communities are shaped by abiotic environmental conditions and biotic interactions, which limit or promote species through physico-chemical growing conditions, disturbances, and interactions, such as competition, facilitation, herbivory, and mutualism across trophic levels (Franklin et al. 2016; Götzenberger et al. 2012; Nabe-Nielsen et al. 2017). Because of low productivity and harsh conditions, high-latitude plant communities are often species poor and typically include one or two highly abundant, dominant species and a small number of subordinate species. Dominant plant species are often most suited to prevailing abiotic and biotic conditions, and they drive biomass production and other main functions provided by communities (e.g., Grime 1998; Hillebrand et al. 2008).

Because community changes are complex, simplified, straightforward metrics, such as species richness, are often used for temporal comparisons (Valdez et al. 2023). However, it is also important to understand how species abundances are distributed and changing in the community, which is measured by species evenness. Changes in evenness reveal changes in dominance patterns. Community-level biodiversity measurements can be further divided into taxonomic, phylogenetic, and functional diversity (Petchey & Gaston 2006; Purvis & Hector 2000). Considering multiple metrics simultaneously should provide a more comprehensive understanding of biodiversity change, yet such approaches remain relatively uncommon (Dornelas et al. 2023).

Importantly, communities are dynamic and undergo constant changes (Lalechére et al. 2025), which are controlled by both abiotic and biotic conditions and stochasticity. Changes in community composition are naturally driven by population changes

(i.e., reproduction, mortality, and dispersal). However, global change rapidly alters high-latitude ecosystems and affects which species thrive and which species decline (e.g., Franklin et al. 2016; Graae et al. 2018; Parmesan & Hanley 2015). This happens through, for example, changes in temperatures and precipitation, altered disturbance regimes, habitat loss, and knock-on effects via changing biotic interactions (Chapin et al. 2000; Tilman 1988). These pressures can ultimately cause high turnover in plant community composition along with losses and gains of populations (Dornelas et al. 2014; Whittaker 1972), but turnover rate varies among environments and across geographical gradients (Blowes et al. 2019).

Turnover in plant communities is generally slow in high-latitude ecosystems, especially in the tundra. This is because of nutrient-poor soils, slow nutrient cycles, cold conditions with low energy input, and short growing seasons, which together favor long-living species resilient to harsh conditions (Becher et al. 2018; Schimel & Bennett 2004). Therefore, the recruitment of new individuals and species is slow (e.g., Eskelinen 2010), and compositional changes also arise slowly. Indeed, despite the expectation of high turnover under rapidly advancing climate change (e.g., Pinsky et al. 2025), high-latitude ecosystems generally show high resistance against climate change (e.g., Virtanen et al. 2010; Wilson & Nilsson 2009), which may relate to both underlying environmental conditions and the composition of species communities. Likewise, in forests, canopies may further buffer the effects of climate change on understory plants by stabilizing microclimatic variation (De Frenne et al. 2019). However, boreal forests are also subject to a wide range of anthropogenic disturbances, including forestry, overexploitation, and forest conversion for other land use, which may drive more rapid changes than in tundra ecosystems (e.g., Franklin et al. 2016; Kaarlejärvi et al. 2021).

Predicting how global change will affect high-latitude plant communities and their diversity is not straightforward, because multiple overlapping and counteracting processes can occur simultaneously. Consequently, plant diversity may either increase or decrease (see e.g., García Criado et al. 2025b) depending on the balance between increasing and decreasing species, whether species that are gaining abundance are novel to local communities (e.g., Steinbauer et al. 2018), and whether they were already widespread or abundant (McCune & Vellend 2013; Olden & Rooney 2006). Raising temperatures should increase energy input and disrupt physico-chemical cycles by, for example, increasing nutrient cycling and flows (Pold et al. 2021) and vegetation productivity (Berner et al. 2020). Concurrently, previously limiting winter temperatures (e.g., Niittynen et al. 2020a) may rise. Improved growing conditions benefit competitive plant species (e.g., Prager et al. 2020) and harm species adapted to harsh conditions, such as arctic species, lichens, and bryophytes (e.g., Bjorkman et al. 2019). Conversely, disturbances may become more frequent and severe if extreme weather events occur more often (Aalto et al. 2026). In addition, the effects of warming temperatures on these communities interact with changes in precipitation and snow conditions (e.g., Niittynen et al. 2020a, 2020b) and can be further modified by plant interactions and herbivory (e.g., Stark et al. 2023a).

In addition to taxonomic composition, global change can shift functional composition (e.g., Niittynen et al. 2020b) and species functional trait variation within communities (e.g., Bjorkman et al. 2018). Functional traits are measurable characteristics of organisms that relate to, for example, plant growth and resource use (e.g., plant height and leaf and root traits); as such, they are linked to species' responses to environmental change and their effects on ecosystem functioning (e.g., Violle et al. 2007). Traits have been successfully linked to community changes, thus resulting in improved understanding

of drivers, community responses, and the ecological consequences of community change (e.g., Bjorkman et al. 2018; Bruelheide et al. 2018). Alterations in taxonomic and functional community composition can cascade through ecological networks (Cirtwill et al. 2018) and disrupt ecosystem functioning on multiple spatial scales (Mekonnen et al. 2021; Schmidt et al. 2024). These can lower ecosystems' resilience against further change (e.g., Isbell et al. 2011; Loreau et al. 2021) and reflect all the way down to human health and well-being (Cardinale et al. 2012; IPBES 2019).

## 2.2 Approaches for collecting long-term vegetation data

Continuous monitoring of vegetation is under threat at a time when the need for long-term observations is greater than ever (Christensen et al. 2020; Mihoub et al. 2017; Nelson 2026). Such time series are essential for ruling out transient changes (Gonzalez et al. 2016; Saccone & Virtanen 2016; Walker et al. 2010) and for alleviating the problem of shifting baselines (Dellavalle et al. 2026; Gonzalez et al. 2016; Montràs-Janer et al. 2024; Soga & Gaston 2018), which are typical in short-term studies. However, long-term, field-based time series remain rare, and existing monitoring efforts are both geographically limited and biased toward accessible areas, leaving many remote and sparsely populated regions unmonitored (see also Bowler et al. 2025).

Beyond long-term monitoring, several approaches exist for studying vegetation change over time. Commonly used methods include vegetation resurveys and remote sensing, which enable direct temporal comparisons (Dornelas et al. 2023), as well as approaches based on a single vegetation observation, such as dendrochronology (e.g., Myers-Smith et al. 2015; Vuorinen et al. 2022) and space-for-time substitution (Lovell et al. 2023), which provide indirect estimates of vegetation change. While indirect approaches help fill knowledge gaps, they cannot replace the direct temporal information provided by repeated sampling. This limitation is particularly relevant for space-for-time substitution, which infers temporal change from environmental gradients, such as elevation, and may either underestimate (Damgaard et al. 2019) or overestimate (Elmendorf et al. 2015; see also Bjorkman et al. 2018) actual vegetation changes.

Among the direct approaches, vegetation resurveys provide valuable insights into long-term vegetation change (Hédl et al. 2017; Kapfer et al. 2017). They involve relocating and resampling historical vegetation plots. The accuracy of plot location information determines whether vegetation resurvey data can be classified as permanent, quasi-permanent, or non-permanent (Kapfer et al. 2017). This classification influences both the type of ecological information that can be drawn from resurvey data and the analytical methods that can be applied. Vegetation resurvey data can also be integrated with other sources of ecological information (Hédl et al. 2017), such as by linking them with databases of species traits.

There are also challenges related to vegetation resurveys (e.g., Kapfer et al. 2017; Stuble et al. 2021). For example, while providing highly valuable information on long-term changes—sometimes extending back beyond the onset of continuous monitoring programmes—they are often less well suited for inferring the causes and consequences of global change, for which experimental studies are needed. Instead, vegetation resurveys are best suited for detecting vegetation changes that are sufficiently large to outweigh the uncertainty associated with plot relocation and observer-related errors (Stuble et al. 2021). Together, observational and experimental approaches provide complementary insights and are both needed to understand and predict the impacts of global change on plant communities (e.g., Bjorkman et al. 2020).

## 2.3 Scale dependence of vegetation changes

Vegetation changes can be measured across multiple scales, from the local and landscape levels to the regional and global levels. Spatial scale has become increasingly important in the context of global change because observed biodiversity changes often depend on the scale of observation. Ecological research would therefore benefit from greater attention to spatial scale (e.g., Chase et al. 2019; Dornelas et al. 2023), particularly its two key components: grain and extent. Grain refers to the size of the observational unit (e.g., the size of a vegetation plot), whereas extent refers to the total area from which vegetation is sampled and analyzed (Wiens 1989). In biogeographical and macroecological research (e.g., McGill 2019), study extent usually ranges from the landscape and regional levels—where biogeographical processes, such as dispersal, become important—to the continental and global levels, at which broad climatic gradients and biogeographical history dominate.

Grain can vary from local to larger spatial levels depending on the studied taxa, region, processes, and research questions, but it is typically small relative to the study extent (Levin 1992). For example, although plant communities as observational units typically occupy a limited spatial area (i.e., they are often measured at a local grain), the choice of study extent can influence the temporal trends inferred from these data (Blowes et al. 2019; Chase et al. 2019). When a large spatial extent is used, patterns and trends can be examined across multiple grain sizes (e.g., plot and landscape-level grain), thereby allowing an assessment of scale dependence in observed vegetation change (Chase et al. 2018). Understanding how scale and environmental gradients jointly shape geographical patterns of biodiversity and ecosystems lies at the core of biogeography. The following sections 2.3.1 and 2.3.2 outline two scale-dependent considerations that are particularly relevant to the thesis and its studies (Studies I–III).

### *2.3.1 Alpha (α) and beta (β) diversity changes as examples of scale dependence*

Researchers often need to reduce multidimensional plant community information into one-dimensional summaries using biodiversity metrics. Although both space and scale are key concepts for interdisciplinary fields rooted in geography and ecology, biodiversity change research frequently operationalizes spatial scale by the partitioning of biodiversity into α (within-community), β (between-community), and γ (regional) components (Jost 2007; Lande 1996; Whittaker 1972).

The α component includes commonly used community diversity metrics, such as species richness, evenness (e.g., Pielou's *J*), and measures that integrate both aspects, including Shannon entropy and Hill numbers (true diversity; Jost 2007). Although α-diversity is measured at small grain sizes (e.g., the plot or community level), it does not imply a small spatial extent. The γ-dimension refers to the sum of local diversity (e.g., total number of species found across communities) within a landscape, region, or other geographically large extent.

β-diversity measures how communities differ in space or time (Whittaker 1972). In its original formulation, it quantifies compositional differentiation among communities through multiplicative partitioning of diversity (true β-diversity; Jost 2007; Tuomisto 2010), but it has been operationalized using a range of distinct approaches, including measures of turnover and compositional variation (Anderson et al. 2011; Tuomisto 2010). When considering temporal differences (i.e., change or trend) in β-diversity, it is often understood either as directional community turnover between time points (e.g.,

Dornelas et al. 2014; Magurran et al. 2019) or as changes through time in the compositional variation among communities, that is, temporal change in spatial β-diversity (e.g., Anderson et al. 2011; McGill et al. 2015). High β-diversity, or compositional dissimilarity among communities, is maintained by environmental and landscape heterogeneity (Stein et al. 2014; Tscharntke et al. 2012), which can be lowered by global change drivers (e.g., climate change-driven easing of local growing conditions and disturbance patterns in cold environments). When communities become more similar to each other, i.e., when compositional similarity increases, they go through a process known as biotic homogenization (Olden & Rooney 2006). Conversely, increased compositional dissimilarity between communities is referred to as biotic heterogenization or differentiation (Olden & Rooney 2006).

Importantly, homogenization can occur even when α-diversity increases because these metrics capture different dimensions of biodiversity at different spatial scales (Finderup Nielsen et al. 2019; Magurran et al. 2018; McCune & Vellend 2013; Montràs-Janer et al. 2024). Homogenization can occur either because of the loss of species or the increase of species already common within communities (McCune & Vellend 2013; Olden & Rooney 2006). The latter process can lower β-diversity by shifting the dominance pattern from local to regional dominance (Hillebrand et al. 2008) while simultaneously increasing α-diversity with increased evenness.

### *2.3.2 High-latitude vegetation change: a matter of extent?*

A distinctive feature of biodiversity change is that commonly used metrics do not show uniform changes across geographical regions, and positive and negative trends often offset each other, thereby resulting in no change at the larger scales (e.g., Blowes et al. 2019, 2024; Dornelas et al. 2014, 2023; Vellend et al. 2013, 2017; see also Chase et al. 2019; Gonzalez et al. 2016). A similar pattern has been observed in tundra plant communities, where species richness and community dissimilarity did not change at the circumpolar scale despite high local turnover in community composition (García Criado et al. 2025b; see also Blowes et al. 2019; Dornelas et al. 2014). Changes in biodiversity metrics can also reflect changes in total abundance (e.g., Blowes et al. 2022; Gotelli et al. 2017) in addition to species-level abundance losses and gains. As a result, studies may report differing biodiversity patterns depending on the chosen spatial grain, extent, and biodiversity metric (e.g., Chase et al. 2019).

Shifts in vegetation can differ greatly across regions (Franklin et al. 2016; Myers-Smith et al. 2020; Vellend et al. 2017). Observational evidence points toward arctic greening (e.g., Berner et al. 2020; Myers-Smith et al. 2020), shrubification (Mekonnen et al. 2021; Myers-Smith et al. 2015), borealization (García Criado et al. 2025a), thermophilization (Elmendorf et al. 2015), and forest advancement (Berner & Goetz 2022; Feng et al. 2026). However, although a trend is often found at the circumpolar scale, these studies also show great heterogeneity in how vegetation responds in different localities (see also Bjorkman et al. 2020; Roland et al. 2021; Verdonen et al. 2026).

Heterogeneity in tundra vegetation responses may be prompted by, for example, differing environmental conditions and differences in the composition of plant species and growth forms (Berner et al. 2020; García Criado et al. 2025a, 2025b; Mekonnen et al. 2021; Myers-Smith et al. 2015, 2020). Functional trait-based studies support this, finding little consistency in community trait changes (Bjorkman et al. 2018) or traits of winner and loser species (García Criado et al. 2023; but see increasing shrub height in Bjorkman et al. 2018). While trends differ along environmental gradients,

signs point toward a particularly fast rate of change in moister (Bjorkman et al. 2018; García Criado et al. 2025a; Myers-Smith et al. 2015) and warmer sites (Elmendorf et al. 2012a; García Criado et al. 2025a) and in regions with faster or higher temperature increases (Elmendorf et al. 2015; García Criado et al. 2025b; but see Elmendorf et al. 2012a, 2012b). However, changes in vegetation are generally not as fast or consistent as expected based on experimental studies (e.g., Bjorkman et al. 2020; Elmendorf et al. 2012a; Henry et al. 2022; but see Elmendorf et al. 2015).

Focusing on regional rather than circumpolar extents allows studies to better resolve region-specific patterns of vegetation and biodiversity change, provided that key gradients within the study region are adequately represented (Bowler et al. 2025; Dornelas et al. 2023; Gonzalez et al. 2016; Valdez et al. 2023). Region-specific focus is also required for more effective conservation and management policies (Moersberger et al. 2024; Wyborn & Evans 2021).

## 3 Aims of the thesis

The overall aims of this thesis are to study what are the main long-term vegetation trends observed in Northern Fennoscandia based on the evidence from repeated samplings and whether these trends align with, diverge from, or remain ambiguous in comparison to circumpolar and boreal evidence. The findings can improve the understanding of long-term vegetation change in a biogeographical transition zone between boreal forests and Arctic tundra.

The thesis includes three research articles (Studies I–III), of which Studies I and II are empirical studies and Study III is a systematic literature review. The two empirical studies examine long-term changes in plant communities using observational vegetation resurvey data from boreal-Arctic heathlands and tundra and boreal forests first sampled over five decades ago across a geographical gradient covering extensive areas in Northern Finland and Northern Norway.

First, a comprehensive view on biodiversity change from heathlands and tundra is provided (Study I, Appendix 1). Second, these data are applied to infer how vegetation shifts reflect in plant community composition in terms of different pollination strategies (Study II). Third, Study III synthesizes long-term vegetation changes of more than ten years based on repeated sampling data in Northern Fennoscandia to provide a regional perspective of long-term trends, which also complements the findings of Studies I and II.

Study I investigates whether the alpha (α) and beta (β) diversity of heathlands and tundra plant communities have changed over time and which species or taxa are linked to changes in diversity. Changes are examined across the whole study region and along three environmental gradients (biogeographical zone, continentality, and habitat type) to answer the following research question (RQ):

> **RQ1**: How have plant communities in heathlands and tundra changed over time in terms of species composition, richness and evenness (α-diversity), and compositional dissimilarity (β-diversity)?

Study II (Appendix 3) investigates how the abundance of pollinator-dependent and pollen and nectar-rewarding plants (hereafter, pollen-nectar plants) have changed in heathlands and tundra and in boreal herb-rich forests over five decades in comparison to plants that do not interact with pollinators (pollinator-independent and non-nectar plants).

The specific research question is as follows:

> **RQ2**: How do changes in vascular plant communities influence the prevalence of pollinator dependence and pollen-nectar provision in forests and tundra?

Study III (Appendix 5) aims to synthesize previous research on decadal (≥ 10 years) vegetation changes in Northern Fennoscandia based on a systematic literature review. It examines evidence gained from repeated samplings from four main terrestrial ecosystems in the region: heathlands and tundra, northern boreal coniferous forests, mountain birch forests, and peatlands. The review expands from compositional changes (Studies I and II) by also providing information about changes in, for example, vegetation productivity, phenology, and distribution, and discusses knowledge gaps related to field-based observational data in Northern Fennoscandia. Evidence from the empirical papers (Studies I and II) is compared with findings from the literature review (Study III) and placed in the context of broader circumpolar and boreal trends associated with climate change. The research question for Study III is as follows:

> **RQ3**: What kind of long-term changes have occurred in the vegetation of Northern Fennoscandia in its four main ecosystems?

Together, these three studies provide strong long-term evidence and a synthesis of vegetation trends in the region of Northern Fennoscandia. The combined use of resurveyed community data and regional focus has thus far been relatively limited in the study area, despite being well suited for detecting biodiversity shifts that are both spatially extensive and ecologically detailed. Along with documenting the current and past state of vegetation, this thesis provides much-needed temporal information about bryophytes and lichens (Studies I and III) and functional changes (Study II) that have to date remained understudied not only in Northern Fennoscandia but also elsewhere at high latitudes.

## 4 Study area

Northern Fennoscandia, located in Northern Europe (Fig. 1), is one of the most studied regions within the circumpolar and boreal belts (Callaghan et al. 2022; Metcalfe et al. 2018; Virkkala et al. 2019). According to Ahti et al. (1968), the main vegetation zones include northern parts of the boreal biome, the boreal-tundra forest transition zone, and the low-arctic and alpine tundra. However, vegetation types are not restricted to individual zones; rather, the region comprises boreal and mountain birch forests, and treeless heathlands and oroarctic tundra (*sensu* Virtanen et al. 2016), along with the peatlands.

The northern boreal forests of the region are dominated by the evergreen coniferous trees Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*). These boreal heath forests grow on relatively dry and nutrient-poor soil, and their understory typically comprises dwarf shrubs, bryophytes, and lichens. On the other end of the productivity gradient, boreal herb-rich forests represent moister forest types that grow on nutrient-rich soil and bedrock, which permits a higher number of species and higher cover of forbs and graminoids than heath forests. However, their distribution is scattered, and they occur in small patches. In the north and along the Scandes, tree lines consist

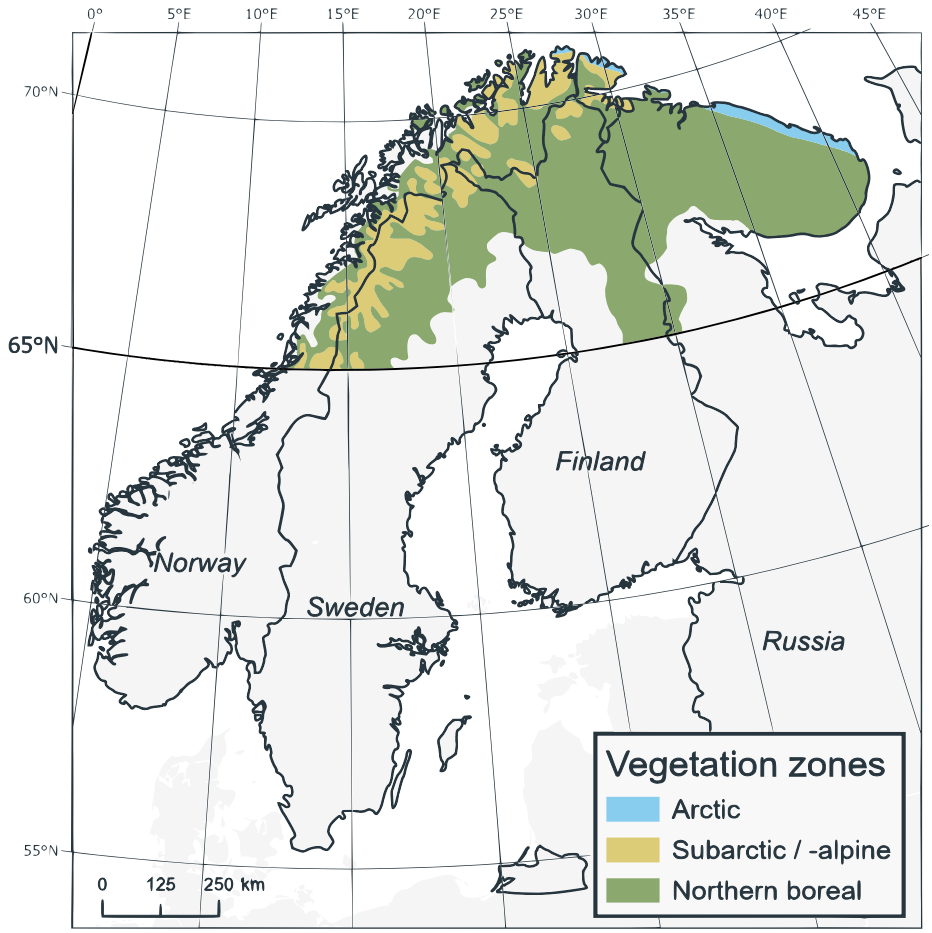


**Figure 1.** Map of Northern Fennoscandia, located north of 65° N and encompassing the northern boreal, subarctic and subalpine, and arctic vegetation zones. The zonation is based on Ahti et al. (1968). Map by Terhi Ala-Hulkko and Petteri Kiilunen.

of mountain birch forests (*Betula pubescens* ssp. *czerepanovii*), which form a narrow but important ecotone between the boreal forest and tundra (Kuuluvainen et al. 2017).

Treeless heath and tundra vegetation in Northern Fennoscandia share characteristics with arctic and alpine environments (Virtanen et al. 2016). Most of the vegetation is dominated by dwarf shrubs and resembles the community composition of dwarf shrub tundra in the Circumpolar Arctic Vegetation Map (CAVM; Walker et al. 2005). Dominant dwarf shrubs include crowberry (*Empetrum nigrum*), bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), bog bilberry (*Vaccinium uliginosum*), dwarf birch (*Betula nana*), and common heather (*Calluna vulgaris*), while bryophytes and lichens form a substantial and often species-rich ground layer (Haapasaari 1988). Community composition is shaped by local variation in terms of, for example, microclimate, elevation, topography, soil moisture and nutrients, and snow patterns. Although they also occur in dry and nutrient-poor heaths, forbs and graminoids (grasses, sedges, and rushes) are often abundant in more productive or wet tundra vegetation types, including snowbeds, tundra meadows, and grass heaths. A key difference compared to most arctic

and subarctic environments is that the numbers of semi-domesticated reindeer are particularly high (Stark et al. 2023a), having risen drastically in recent decades (Bernes et al. 2015).

## 5 Materials and methods

### 5.1 Temporal plant community data (Studies I and II)

Extensive spatial and temporal resurvey data on terrestrial plant communities from Northern Fennoscandia are used in Studies I and II. The data contain species-specific percentage cover values for vascular plant, lichen, and bryophyte species in oligotrophic heathlands and tundra recorded from 2 x 2-meter vegetation plots (Studies I and II) and for vascular plants in herb-rich forests recorded from 5 x 5-meter plots (Study II). The heathland and tundra sites were originally sampled between 1964–1975 by Haapasaari (1988), and herb-rich forest sites between 1968–1975 by Kaakinen (1971, 1974, 1974–1975). The sites were resurveyed from 2010 through the 2020s (Bråthen et al. 2024; Bockelie Rosendal 2024; Happonen et al. 2013–2020, 2021; Maliniemi 2019–2020; Maliniemi et al. 2018). All the sites were undisturbed by human land use during the original survey. These represent pioneering datasets in terms of spatial coverage, especially for the heathlands and tundra of Northern Fennoscandia, compared to many other datasets that are local and generally cover much shorter timescales (see Study III for a review).

In Study I, 217 plots resampled in 2013–2020 (Maliniemi 2019–2020; Maliniemi et al. 2018) are supplemented by 58 plots resurveyed in 2023 (Bockelie Rosendal 2024), thus totaling 275 plots. None of the sites was disturbed by human land use during the study period. In Study II, the total number of plots from heathlands and tundra is 419, of which 347 are undisturbed, along with 72 disturbed plots (Maliniemi 2019–2020; Maliniemi et al. 2018; Bråthen et al. 2024). For herb-rich forests, the total number of plots is 286, of which exactly half (143 plots) are undisturbed and the other half disturbed (Happonen et al. 2013–2020, 2021). "Disturbed" refers to plots resurveyed in sites that had experienced at least some magnitude of visible human land use after the original survey (e.g., forestry in herb-rich forests and ski-resort building and maintenance in tundra).

In Study I, site classifications provided by Haapasaari (1988) are used to test whether vegetation responses differed along environmental gradients, namely biogeographical zone, continentality, and habitat type. The biogeographical zones were the northern boreal (plot n = 96), hemioroarctic (n = 84), and oroarctic vegetation types (n = 95). Continentality describes local humidity (rather than direct distance to the ocean) and consists of the subcontinental (i.e., characterized by high bryophyte cover; n = 47), indifferent (similar bryophyte and lichen cover; n = 111), and oceanic (high lichen cover; n = 117) vegetation types. Habitat types are based on dominant dwarf shrub species and include the *Empetrum nigrum* (n = 104), *Vaccinium myrtillus* (n = 87), *Calluna vulgaris* (n = 29), *Betula nana* (n = 31), and the relatively barren windswept types (n = 24). The numbers of plots represent the actual prevalence of each habitat type across the oligotrophic heathlands and tundra of Northern Fennoscandia. All of these gradients were independent of each other, meaning that, for example, different continentality classes occurred across all biogeographical zones, and none of the classes is limited to a certain geographical area (Appendix 2: Fig. S1).

Study II relied on species-level ecological indicator values (EIVs; Tyler et al. 2021) to classify vascular plants according to their pollinator dependence and pollen and nectar production. The species cover in each plot is summed for these functional groups (pollinator-dependent versus pollinator-independent and pollen-nectar versus non-nectar plants) and further aggregated by plant growth form (deciduous and evergreen shrubs, forbs, graminoids, and pteridophytes).

## 5.2 Methods

In Study I, species richness and evenness (Pielou's *J*) are selected for the α-diversity measures. Instead of β-diversity as differentiation in the strict sense of multiplicative partitioning (*sensu* Jost 2007; Tuomisto 2010; Whittaker 1972), temporal changes are measured in terms of change in compositional variation using dissimilarity-based measures. This approach shows whether communities have gone through homogenization or heterogenization. The community dissimilarity measure is based on species percentage covers and Bray-Curtis distances. For species-level temporal changes, absolute species cover was used to account for actual increases and decreases in species-specific covers.

Temporal changes in species richness, evenness, and species covers are analyzed using permutated t-tests (Legendre 2019). Temporal changes in compositional dissimilarity are analyzed based on the multivariate homogeneity of group dispersions (Anderson et al. 2006) and quantified as changes in the average distance of plots to survey-specific spatial medians. All the responses (species richness, evenness, compositional dissimilarity, and species-level changes) are analyzed across all sites and species and then separately for all environmental gradients (biogeographical zones, continentality classes, and habitat types) and vascular plants, bryophytes, and lichens. The compositional shifts of habitat types are visualized with principal coordinate analysis ordination plots.

In Study II, temporal changes in the absolute cover of plant groups are analyzed using hierarchical Bayesian regression models (Bürkner 2017). These analyses are conducted for all plant groups. Temporal changes in pollinator-dependent, pollinator-independent, pollen-nectar, and non-nectar plants (i.e., species that do not produce either pollen or nectar) are analyzed in relation to time and human land-use disturbance, whereas only time is included in the analyses of plant growth forms. Random effects of plot identity and geographical region are included in all models to account for repeated measurements and spatial variation, respectively. All statistical analyses are performed in the R software (R Core Team 2025).

In Study III, a systematic literature review is conducted following the PRISMA guidelines adapted for studies in ecology and evolution (PRISMA-EcoEvo; O'Dea et al. 2017). The review aims to synthesize research on long-term (≥ 10 years) vegetation changes in Northern Fennoscandia based on repeated samplings across its main terrestrial vegetation types (heathlands and tundra, boreal and mountain birch forests, and peatlands). The review includes field sampling and remote sensing (RS) studies in which temporal change was assessed using data gained through repeated sampling (i.e., vegetation measured at least twice through time), while experimental manipulations or indirect proxies of vegetation change (e.g., the space-for-time approach) are excluded (see Appendix 6: Table S1 for detailed exclusion criteria). The included studies were published between 1990 and 2025.

# 6 Results

## 6.1 Changes in community composition and α- and β-diversity in heathlands and tundra (RQ1)

Study I showed that plant communities in heathlands and tundra have undergone biotic homogenization across Northern Fennoscandia over the past five decades, which was reflected in increased compositional similarity (i.e., decreasing β-diversity; Figs. 2a and 2b). At the same time, species richness remained stable or increased slightly depending on the taxa, while evenness increased, indicating changes in α-diversity. These temporal trends in both α- and β-diversity were largely consistent across biogeographical zones and along the continentality-humidity gradient, with the exception of the subcontinental zone of the latter. Among the habitat types, homogenization was observed only in *B. nana*-type communities, and this was the only habitat type that showed no significant species-level changes.

Of the different growth forms, the vascular plant and lichen communities showed homogenization, whereas the bryophyte communities were generally more stable and showed only a weak homogenization trend across all sites (Fig. 2a). Among the different habitat types, homogenization was observed only in lichen communities. Vascular plant community evenness and richness increased slightly. Evenness increased especially in the northern boreal zone, and both evenness and richness increased at indifferent sites. In contrast, lichen richness decreased in the northern boreal zone and indifferent sites, whereas lichen evenness increased across the biogeographical zones and along the continentality-moisture gradient, except in the northern boreal zone and oceanic sites.

Across all sites, crowberry cover increased strongly across the study area, being the most pronounced species-specific change. Other species-level cover changes were generally small, but differing patterns were found across biogeographic zones, the continentality-moisture gradient, and habitat types. At the habitat-type level, crowberry

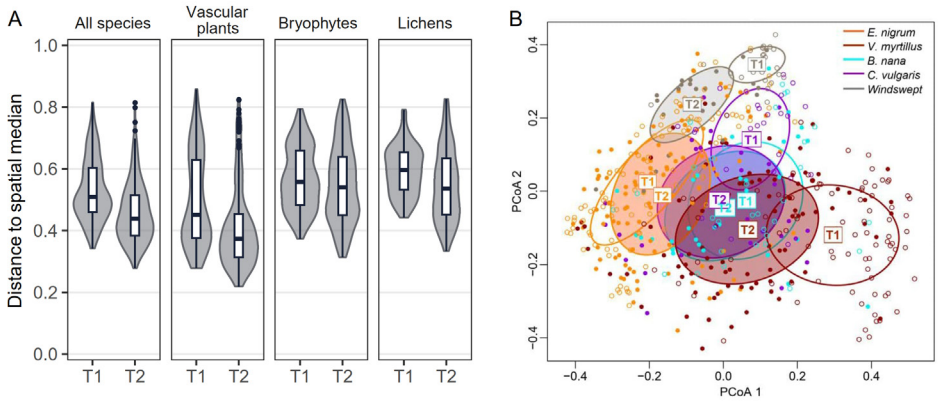


**Figure 2.** Compositional change in vegetation between the original 1960s survey (T1) and the 2010s resurvey (T2) in Study I. (A) Distance to the spatial median (a measure of compositional dissimilarity) at T1 and T2, shown for all species combined and separately for vascular plants, bryophytes and lichens. (B) Principal coordinates analysis (PCoA) of Bray-Curtis dissimilarities calculated from species percentage cover data, with sites (points) colored by habitat type. Labels indicate the spatial median of each habitat type at T1 and T2. Ellipses represent one standard deviation of site scores for each habitat type.

cover did not increase in *E. nigrum*-type or *B. nana*-type communities, but it encroached strongly in habitats dominated originally by bilberry and heather as well as in windswept sites (Fig. 3), becoming the dominant species by the resurvey.

Previously common bilberry-dominated habitats shifted toward the *E. nigrum*-type (Fig. 2b), and the windswept types harbored more extensive crowberry cover than in the 1960s. Increases in evergreen shrub species other than crowberry were only very modest or even negative. Some deciduous shrubs increased slightly in cover across the study area (e.g., dwarf birch and *Vaccinium uliginosum*), whereas bilberry cover decreased, especially in the *V. myrtillus* type (Fig. 3). Bryophyte species *Pleurozium schreberi* increased markedly across all sites, but mostly in *C. vulgaris*-type communities. Lichen cover decreased, especially in subcontinental zones, and it was linked particularly to a decrease in *Stereocaulon* spp.

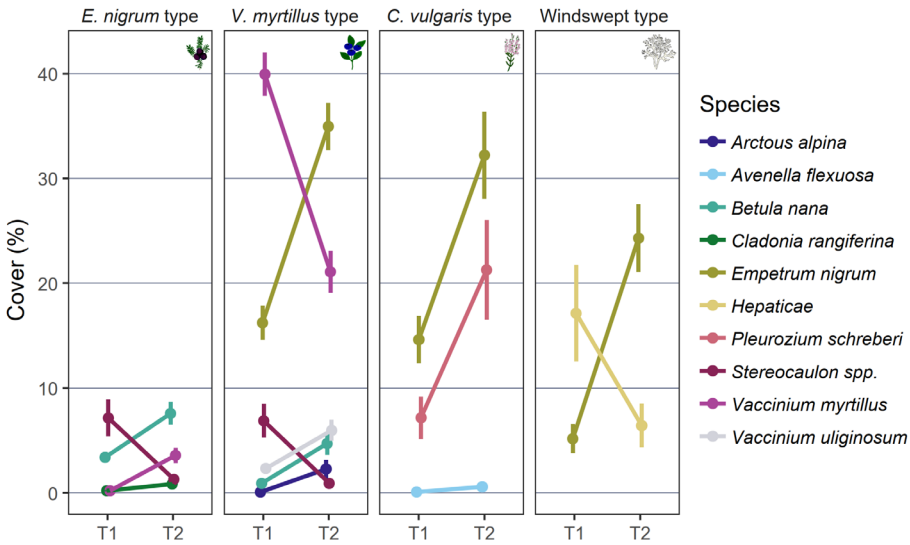


**Figure 3.** Change in mean species percentage cover between the original 1960s survey (T1) and the 2010s resurvey (T2) in Study I, shown separately for habitat types classified according to their dominant species at T1 (crowberry/*E. nigrum* type, bilberry/*V. myrtillus* type, and heather/*C. vulgaris* type), as well as for windswept type. Only species showing statistically significant temporal changes in mean cover are shown, based on paired permutation t-tests (9999 permutations) with Holm correction for multiple testing. No significant changes were detected in *Betula nana*-type habitat, which is therefore not shown. Error bars represent 95% confidence intervals.

## 6.2 Prevalence of pollinator dependence and pollen-nectar provision (RQ2)

Study II showed a decline in the prevalence of pollinator dependence in heathlands and tundra and herb-rich forests (Fig. 4). No significant effect of land use disturbance on these trends was found, suggesting a pervasive trend not controlled by land use. In heathlands and tundra, species cover increased across all plant groups (pollinator-dependent and independent plants as well as pollen- and non-nectar plants); however, the increase was substantially stronger for pollinator-independent and pollen-nectar plants. Among growth forms, the strongest increase was found in pollinator-independent and non-nectar evergreen shrubs, mainly crowberry (Appendix 3: Table S1), followed by

pollinator-dependent deciduous shrubs (Appendix 3: Fig. 4a). Although pollinator-independent plants were already more abundant at the beginning of the study period, this discrepancy became larger over time. Importantly, because each species group increased in cover, total absolute species coverage increased strongly.

In herb-rich forests, pollinator-dependent and pollen-nectar plants were mostly replaced by species that are both pollinator-independent and do not provide nectar. The decline of forbs (mainly pollinator-dependent and pollen-nectar species) was strong, while pteridophytes and graminoids, which do not interact with pollinators, increased (Appendix 3: Fig. 4b; Appendix 4: Fig. S4). However, slight increases of pollinator-dependent, deciduous shrubs that provide pollen and nectar (Appendix 3: Fig. 4b) alleviated some of the declines in forbs in terms of pollinator dependence and pollen-nectar provision.

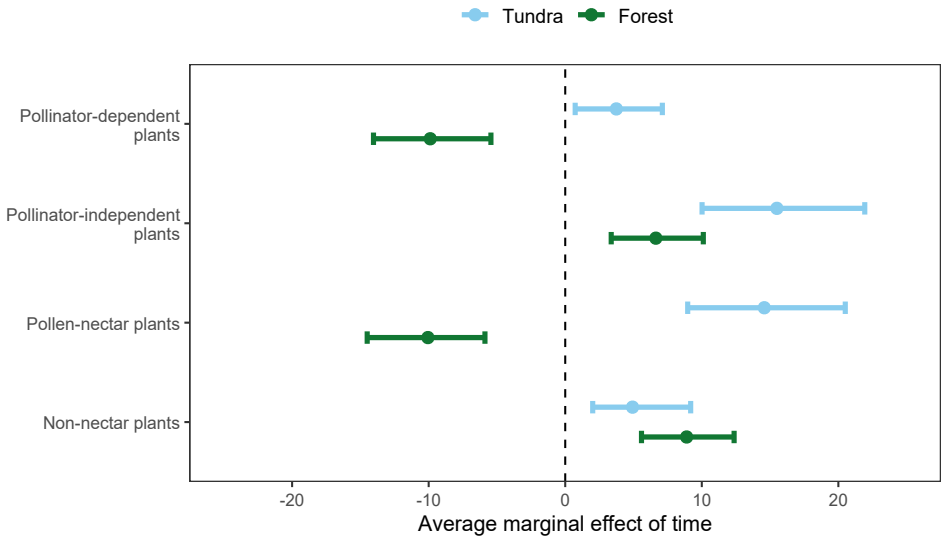


**Figure 4.** Estimated average marginal effects of time on the cover of pollinator-dependent and pollinator-independent plants, and pollen-nectar and non-nectar plants, in heathlands and tundra, and herb-rich forest communities (labeled "Tundra" and "Forest", respectively) in Study II. Points indicate model estimates and error bars indicate 95% confidence intervals.

### 6.3 Review of long-term vegetation change studies in Northern Fennoscandia (RQ3)

Study III showed that, of the 141 studies included in the review, 105 were based on field-based vegetation data, while the remaining studies relied primarily on satellite imagery. Among the countries studied, studies conducted in Finland and Sweden were most common, whereas studies from the Kola Peninsula were rarest. Around 70 % of field-based studies used permanent vegetation plots, while non-permanent plots were also common. Across these studies, the median year of the first sample was 1983, and the last was 2013 (Fig. 5a). Study duration averaged 37 years with a median duration of 24 years. Vegetation was mostly sampled only twice over time, whereas annual or bi-annual time series were rare and largely limited to phenological studies and relatively short-term experimental studies (from which only unmanipulated control plots were included in the review). Changes in community composition were the most frequently studied response, followed by changes in productivity and taxonomic diversity (Fig. 5b).

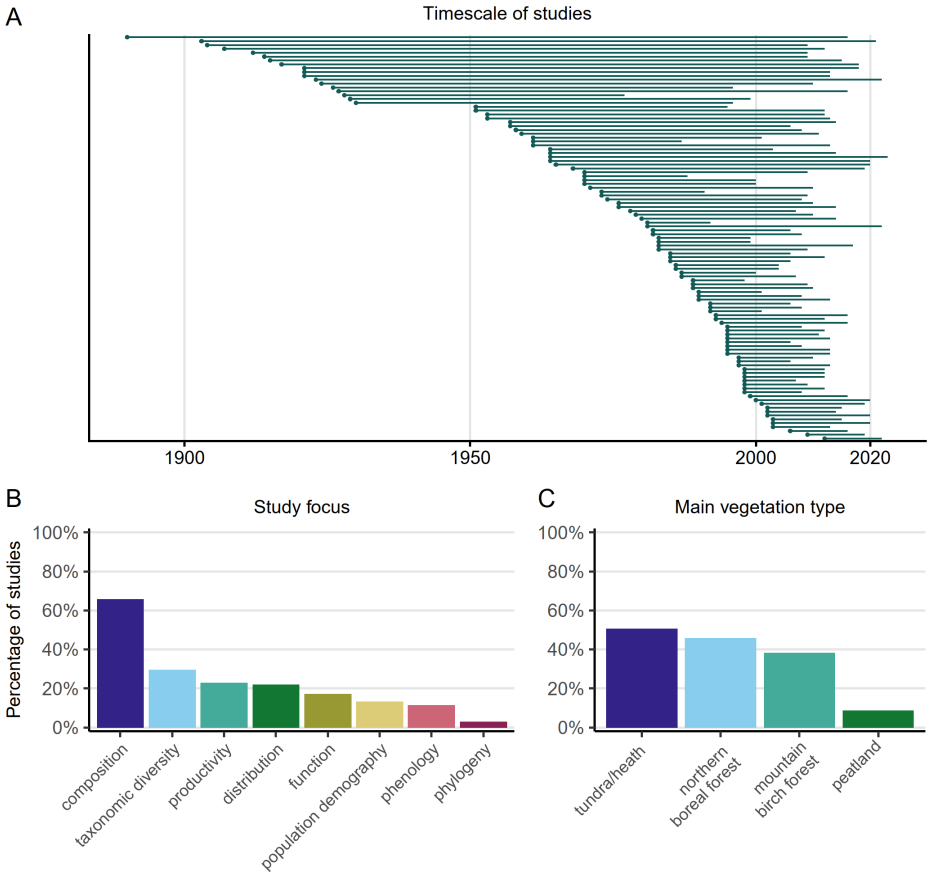


**Figure 5.** Overview of field-based studies (n = 105) included in the systematic review (Study III), summarizing their temporal scope, study focus, and main vegetation types studied. (A) Temporal distribution of datasets, showing the first and last sampling years of each study. (B) Percentage of studies addressing different study foci. (C) Percentage of studies representing different main vegetation types. Because the categories in panels B and C are not mutually exclusive, percentages do not sum to 100%.

Among the main vegetation types, heathlands and tundra were the most studied, followed by coniferous northern boreal forests and mountain birch forests (Fig. 5c). In terms of repeated sampling studies, long-term vegetation change has remained critically understudied in peatlands. Local-scale studies dominated across all vegetation types. There were some differences in the distribution of study foci between vegetation types (Appendix 5: Fig. 7). Only 11 studies specifically considered long-term vegetation changes in peatlands (mires and bogs) and reported turnover toward distinct species composition that was often characterized by an increasing dominance of graminoids. The RS studies showed an overall increase in productivity based on remotely sensed vegetation greenness indices, but both productivity and phenology showed high spatial and temporal heterogeneity in terms of their responses.

Most of the observed vegetation changes showed considerable heterogeneity within the main ecosystems of Northern Fennoscandia. In heathlands and tundra, a large proportion of studies used plant community data to study the composition

or taxonomic diversity of vascular plant communities. Similarly to Studies I and II, the literature review in Study III revealed that crowberry is encroaching widely in the region (e.g., Bråthen et al. 2024; Tuomi et al. 2024). Deciduous shrub increases were not generally strong or widespread across the study region, which was comparable to Studies I and II, and no increases in tall shrubs were found. Instead, many studies showed stability and even declines of deciduous shrubs, such as dwarf birch, under ambient warming (Eskelinen & Oksanen 2006; Kaarlejärvi et al. 2015). No increases in shrub height or community height were shown in Study III. No directional α-diversity changes were found either, with increases, decreases, and stability being common across vascular plants and non-vascular cryptogams (e.g., Bråthen et al. 2024; Steinbauer et al. 2018; Wilson & Nilsson 2009). Studies that focused on lichen cover and biomass did find lichen declines (Maliniemi et al. 2018; Vuorinen et al. 2017; Wallenius et al. 2025), while bryophytes most often showed stability (but see Graglia et al. 2001; Vowles et al. 2017).

No borealization of tundra communities through the establishment of infrequent boreal species was observed; the species that increased in cover were already common within the communities. Similarly, no loss of arctic species was observed in the empirical studies or in the review. Likewise, no sign of thermophilization occurred (e.g., Vuorinen et al. 2017), although it was rarely explicitly studied (but see Hagenberg et al. 2022). Nor was there clear evidence that tundra or boreal-tundra species are shifting toward higher altitudes (but see MacDougall et al. 2021).

In northern boreal forests, the main findings were related to the effects of forestry and climate change on vegetation. Existing national forest inventory (NFI) programmes that cover Finland, Sweden, and Norway have provided systematic information on long-term changes across each country (e.g., Antão et al. 2022; Hedwall et al. 2021). Old-growth forests have been replaced by younger trees as forestry has intensified and extended into these previously undisturbed and less productive forests (e.g. Korhonen et al. 2021). At the same time, forests have become denser and productivity has increased (e.g., Franke et al. 2015; Henttonen et al., 2019; Hofgaard et al. 2013). Forest understories have been studied less than trees and canopies, but evidence for decline in lichen cover and biomass was clear (Colpaert & Kumpula 2012; Kumpula et al. 2014). Tree lines only advanced locally, but densification of forest vegetation points toward potential future advancement of the tree line (e.g., Franke et al. 2015; Maliniemi et al. 2025).

Studies of mountain birch forests focused most often on the composition and distribution of trees and shrubs. Similarly to boreal heath forests, the tree lines of mountain birch have not markedly advanced across the whole region. Instead, local advances, retreats, and stability were reported in several studies (Hofgaard et al. 2013; MacDougall et al. 2021; Van Bogaert et al. 2011; Vuorinen et al. 2017), which were strongly linked to disturbances, such as reindeer grazing and insect outbreaks. Increases of mountain birch biomass and shrub cover have also led to densification of mountain birch forests (Hedenås et al. 2011; Rundqvist et al. 2011; Tømmervik et al. 2009).

Based on the findings of Studies I–III, four key vegetation trends can be identified across Northern Fennoscandia. These trends, together with the main findings of each study, are summarized in Figure 6.

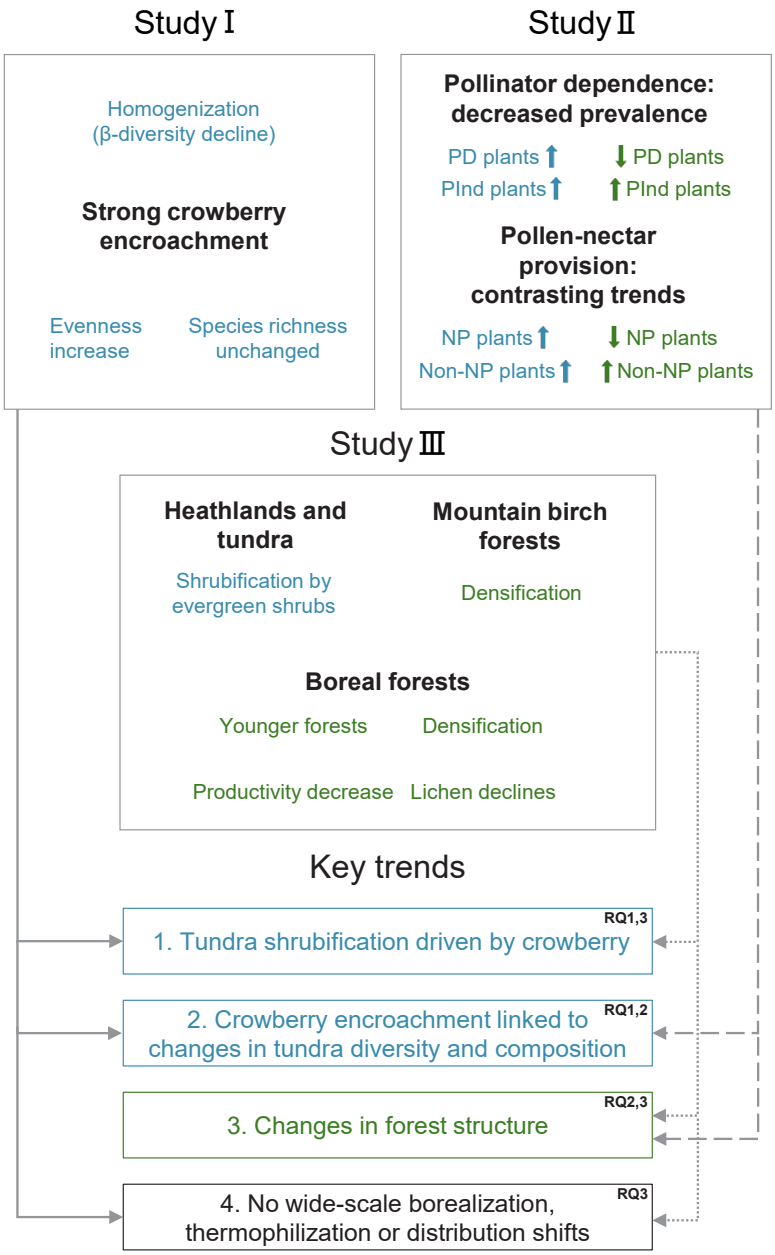


**Figure 6.** Synthesis of the main findings from Studies I–III and their relationships to the four key trends identified in this thesis. Blue text and arrows represent findings from heathlands and tundra, and green text and arrows represent findings from forests. Lines connect study findings to the key trends they support, and line style indicates the originating study (Study I: solid, Study II: dashed, Study III: dotted). Within the Study II panel, arrows ↑ and ↓ denote increasing and decreasing cover, respectively, of pollinator-dependent, pollinator-independent, pollen-nectar, and non-nectar plants over time. Abbreviations: PD = pollinator-dependent plants, PInd = pollinator-independent plants, NP = pollen-nectar plants, Non-NP = non-nectar plants, β-diversity = compositional dissimilarity among communities, RQ1 = research question 1, RQ2 = research question 2, RQ3 = research question 3. RQ labels indicate which research question(s) each key trend is relevant to.

# 7 Discussion

The following sections discuss the results by highlighting four key vegetation trends (Fig. 6) identified across Northern Fennoscandia based on the empirical studies (I and II) and systematic literature review (Study III), along with their wider implications. First, crowberry-driven shrubification in heathlands and tundra found in all of the studies of the thesis is discussed (7.1). The second section (7.2) discusses the impacts of crowberry encroachment on taxonomic (dominance and homogenization) and functional composition (prevalence of pollinator dependence and pollen-nectar provision) of heathlands and tundra. In the third section (7.3), the changing forest structure found in Studies II and III is discussed. The lack of region-wide evidence on borealization, thermophilization, and altitudinal shifts of species are discussed in the fourth section (7.4). The fifth section (7.5) discusses the use of observational long-term data and its limitations, the need for regional perspective in vegetation change studies, and directions for future research.

## 7.1 Key trend 1: tundra shrubification is driven by crowberry

The main finding of the empirical studies (I and II) showed crowberry-driven shrubification of heathlands and tundra. This reflected the broader shrubification trend observed across the circumpolar tundra (Elmendorf et al. 2012; Mekonnen et al. 2021; Myers-Smith et al. 2011, 2015), but it was not driven by deciduous shrubs in Northern Fennoscandia. The literature review (Study III) supported the findings of both crowberry encroachment and an only minor increase of deciduous shrubs in the region, which was similar to Studies I and II. None of the other evergreen shrub species showed major changes in heathlands and tundra across the empirical studies or the review (but see Graglia et al. 2001; Molau 2010). However, studies have also demonstrated the negative effects of extreme events (Bjerke et al. 2017) and small rodent peaks (Olofsson et al. 2013) on crowberry over time, suggesting that such disturbance events can also suppress crowberry expansion.

Circumpolar studies on experimental warming have demonstrated that deciduous shrubs benefit from increased warmth (e.g., Bjorkman et al. 2020; Elmendorf et al. 2015). However, evidence exists that reindeer grazing can slow down shrubification driven by deciduous shrubs, and this applies also to Northern Fennoscandia, where deciduous shrub abundance, height, and biomass are strongly controlled by reindeer grazing (e.g., Kaarlejärvi et al. 2015; Olofsson et al. 2009; Ramirez et al. 2024; Vowles et al. 2017). Yet, reindeer avoid crowberry and other evergreen shrubs due to their low palatability (Tuomi et al. 2024; Vowles et al. 2017) but may trample them.

Shrubification and greening (i.e., increased vegetation productivity, which is often measured as biomass) are closely connected phenomena, but whether shrubification directly leads to greening depends on the traits of the encroaching species and the responses of co-occurring species. Based on the RS studies (Study III), there was a general but inconsistent greening of Northern Fennoscandia that aligned with the circumpolar and boreal trend. This was clearly observed in forests, but little direct change in biomass was found across the field-based studies of heathlands and tundra (but see Olofsson et al. 2009; Tuomi et al. 2024). However, because Tuomi et al. (2024) showed that crowberry encroachment increases community biomass, it should be assumed that evergreen shrubification has led to greening across the region, which they termed evergreening.

Importantly, crowberry alters vegetation structure differently from deciduous shrubs, increasing in cover and biomass through lateral spread rather than vertical growth (Tuomi et al. 2024). This highlights that the shrubification driven by evergreen dwarf shrubs like crowberry likely has different effects and feedbacks on ecosystems compared to deciduous shrubs (e.g., Metcalfe & Olofsson 2015; Vowles & Björk 2019). Crowberry also has strong and often negative effects on other plant species and ecosystem processes (Bråthen et al. 2018; González et al. 2021; Mod et al. 2016; Tuomi et al. 2024; Tybirk et al. 2000), which pose additional threats to, for example, diversity and ecosystem multifunctionality (Hautier et al. 2018; Mori et al. 2018). Despite the potential negative effects of crowberry-driven shrubification, it may also help slow down wider shrubification of taller shrubs, borealization, and soil carbon losses that advance climate change (Bråthen et al. 2018; González et al. 2021; Niittynen et al. 2020b; Vowles & Björk 2019; but see Sundqvist et al. 2020). However, this may be dependent on other factors, including the intensity of reindeer grazing (Ylänne et al. 2020).

### 7.2 Key trend 2: strong linkage between crowberry encroachment and changes in tundra plant community composition and diversity

Crowberry encroachment was clearly linked to both taxonomic and functional changes in mountain heath and tundra communities (Studies I–III). By becoming dominant species across different habitat types, crowberry drove a shift from local dominance by different dwarf shrubs to regional dominance (see also Bråthen et al. 2024), resulting in the homogenization of plant communities (see also Hillebrand et al. 2008). Unexpectedly, crowberry encroachment did not lead to a decline in α-diversity (Bråthen et al. 2018; Mod et al. 2016). On the contrary, vascular plant communities increased in evenness because they were no longer dominated by one but often two species. This finding emphasizes the importance of considering different biodiversity metrics to understand biodiversity change (Dornelas et al. 2023). Interestingly, increased evenness across the study area was driven by crowberry-dominated sites, in which bilberry and dwarf birch increased in cover (Fig. 3). Dwarf birch in particular seems to tolerate competition with crowberry, which may have a wider impact on the shrubification trend in the future.

Study III supported the findings of Study I, highlighting the lack of systematic change in α-diversity across Northern Fennoscandia, similar to a recent circumpolar study (García Criado et al. 2025b). Likewise, no major losses of tundra species were found. Despite no α-diversity trend in reviewed studies, species communities were clearly undergoing temporal turnover (García Criado et al. 2025b).

Whereas Study III showed that the number of long-term functional studies in the region remained low, Study II highlighted a functional consequence of vegetation change, especially regarding the identity of increasing shrubs in heathlands and tundra. It demonstrated how crowberry encroachment is linked to the increased abundance of pollinator-independent and pollen-nectar plants. As crowberry provides abundant pollen but very little nectar, the strong increase in pollen-nectar plant cover likely translates into little change in nectar provision. The decline in bilberry dominance may further limit nectar availability because bilberry is one of the few nectar-rich species in heathlands and tundra (Tyler et al. 2021; Appendix 4: Table S1a and S1c). The increased dominance of nectar-poor crowberry may alter pollinator foraging behavior by increasing the likelihood that pollinators encounter crowberry while searching for floral resources, potentially affecting pollinator foraging patterns and plant pollination

success (Biella et al. 2019; Cirtwill et al. 2018). A key implication of Study II is that the ecological consequences of shrubification depend strongly on the identity of the expanding shrub species. For example, expansion of the *Betula* species, which are pollinator-independent and provide no food for pollinators (Tyler et al. 2021), would likely have neutral or negative consequences for pollinators, whereas expansion of the nectar-rich *Salix* species (Tyler et al. 2021) may promote pollinators. Yet, such shifts may also strongly reshape plant-pollinator networks (Cirtwill et al. 2018).

Simultaneously with crowberry expansion, lichens declined strongly in the study region (Studies I and III) and showed homogenization in common habitat types. While lichen decline has been linked to shrubification, competition with vascular plants (e.g., Bernes et al. 2015; Elmendorf et al. 2012; Hagenberg et al. 2022; Olofsson et al. 2009), and forestry practices (Kumpula et al. 2014), lichens are particularly sensitive to intense reindeer grazing and trampling across Northern Fennoscandia (e.g., Kumpula et al. 2014; Wallenius et al. 2025).

### 7.3 Key trend 3: changes in forest structure

Study III found that northern boreal forests became consistently denser (e.g., Franke et al. 2015; Henttonen et al. 2019) and that their productivity increased (Kauppi et al. 2015), while mountain birch forests also showed densification due to tree and shrub growth (e.g., Rundqvist et al. 2011). The reviewed studies reported wide impacts of forestry practices on forest structure. For example, in northern herb-rich forests, forest management actions have included the removal of deciduous trees and enhanced spruce growth, which increases canopy cover (see Happonen et al. 2021). This alters, for example, light conditions (Muurinen et al. 2019; Tonteri et al. 2016) and likely has a further impact on forest understory communities. Additionally, natural succession and climate warming have likely driven densification of forest vegetation along with the abandonment of traditional land use in these areas (e.g., Tømmervik et al. 2019). It is possible, however, that forest understory responses are still lagging due to canopy buffering (De Frenne et al. 2019).

As demonstrated by Study II, forests can provide an important pollinator habitat, particularly where nutrient-rich soils allow a well-developed, diverse understory with a high cover of pollen- and nectar-rewarding plants, such as forbs (De Schuyter et al. 2024; Proesmans et al. 2019). A loss of pollinator-dependent and pollen-nectar forbs was found in herb-rich forests, which points toward changing light availability (De Frenne et al. 2019; Hedwall et al. 2019, 2021; Tonteri et al. 2016) as well as the effects of reindeer grazing on large forbs (Happonen et al. 2021).

A previous study conducted using a subset of this herb-rich forest data (Happonen et al. 2021) showed that diversity (including evenness) had increased and vegetation height had decreased. Changes in diversity and vegetation height were linked to reindeer density, while successional (canopy) development lowered the vegetation height by lowering the light availability (Happonen et al. 2021). Interestingly, some shift in species dominance in herb-rich forests has likely occurred because the two most abundant tall forbs, *Geranium sylvaticum* and *Filipendula ulmaria*, declined in cover (Study II). However, whether this decreases nectar provision is debatable because both species provide pollen but very little nectar (Tyler et al. 2021), similar to crowberry. More long-term evidence from forest understory communities is clearly needed.

### 7.4 Key trend 4: no wide-scale borealization, thermophilization, or distribution shifts

Considering the location of the study region in the transition zone between boreal and tundra vegetation, the lack of long-term borealization of tundra communities can be considered surprising (see also García Criado et al. 2025a). Increases in cover through Studies I–III occurred for species already abundant and dominant in heathlands and tundra (Haapasaari 1988). Importantly, crowberry—an extremely widespread species—was already the most abundant species, and crowberry-dominated sites were the most common habitat type during the original survey (Studies I and II). Therefore, it would be misleading to treat its encroachment as borealization in the absence of encroachment of originally less-common boreal-tundra or purely boreal species. Studies that directly assess the rate of oroarctic tundra borealization in Northern Fennoscandia are clearly needed and could, for example, follow the approaches suggested by Verdonen et al. (2026). More broadly, existing community composition should be explicitly considered when assessing the rate of borealization across different circumpolar regions (see García Criado et al. 2025a). Nevertheless, emphasis should shift toward evaluating how vegetation shifts modify community-level processes and whether these effects lead to boreal-like ecosystem functioning (Verdonen et al. 2026), independent of how borealization is defined.

Similar to the lack of deciduous shrubification and borealization, no thermophilization (Elmendorf et al. 2015) of plant communities was found, although this was rarely explicitly studied (but see Hagenberg et al. 2022) (Study III). More focused studies on thermophilization are needed in the future by, for example, using data on functional traits (e.g., Bruelheide et al. 2018) or the estimated temperature affinity of species (e.g., Mäkinen et al. 2024; Pacheco-Riaño et al. 2024).

No clear and pronounced altitudinal shift in distribution of tundra species (e.g., MacDougall et al. 2021; Vuorinen et al. 2017; Wilson & Nilsson 2009) or tree and forest lines (e.g., Henttonen et al. 2019; Hofgaard et al. 2013; MacDougall et al. 2021; Van Bogaert et al. 2011) was found in Study III. Several studies suggested that distributional patterns of deciduous trees and shrubs are controlled by reindeer grazing and insect outbreaks (Hofgaard et al. 2013; Olofsson et al. 2013) and that both heath and mountain birch forests may also show strong time lag (Rees et al. 2020). A substantial gap exists among long-term studies on whether species are moving northward or not (but see Antão et al. 2022). This likely relates to the lack of geographically extensive data—except for NFI data—which prevents such approaches but also reflects broader uncertainty regarding circumpolar distribution shifts. Despite circumboreal evidence of tree and forest-line shifts (Berner & Goetz 2022; Rees et al. 2020), evidence of other distributional shifts across tundra remains local (Myers-Smith & Hik 2018; Savage & Vellend 2015).

### 7.5 Future directions and limitations

With a focus on Northern Fennoscandia, this thesis contributes new region-specific evidence to boreal-Arctic research. By revealing both consistencies with and departures from circumpolar trends, it refines our understanding of circumpolar vegetation change. These findings also point to several priorities for future research and monitoring. Accordingly, this final section considers relevant limitations of observational long-term data, outlines key directions for future boreal-Arctic research, and

briefly discusses the benefits of continued long-term monitoring for science, policy, and ecosystem management.

As most compositional and diversity trends in high-latitude ecosystems are not universal in magnitude and direction, causes of heterogeneity need to be considered more carefully in future studies. Both local environmental gradients and underlying community composition can affect vegetation responses (García Criado et al. 2025a; Mekonnen et al. 2021; Roland et al. 2021), as demonstrated by Study I. For example, besides warming and herbivory, changes in snow (e.g., Niittynen et al. 2020a, 2020b) and moisture conditions can be important in tundra. The moisture gradient has been demonstrated to be an important factor for vegetation trends (Elmendorf et al. 2012b; García Criado et al. 2025; Myers-Smith et al. 2015; Scharn et al. 2021), community composition (Kemppinen et al. 2019), trait distribution (Bjorkman et al. 2018), and species richness (Nabe-Nielsen et al. 2017). Furthermore, in Study I, homogenization was strong in the moister oceanic type but absent from drier subcontinental sites, while Study III highlighted declines for wetland, snowbed, and tussock tundra species (Molau 2010; Sandvik & Odland 2014). Moisture gradients can both shape long-term responses and be affected by ongoing shrubification (e.g., Kemppinen et al. 2021) and should be of interest in future research.

Along with regional differences in species communities and environmental conditions, several factors can generate heterogeneity among findings from long-term vegetation studies across boreal-Arctic regions. These sources of variation are relevant to both the empirical studies and review presented in this thesis and to observational vegetation surveys more generally. The use of two time points in the empirical studies of this thesis may have masked processes that occurred between surveys (Staude et al. 2023; Stuble et al. 2021). Relatedly, in the review, the beginning, end, and timescales of the studies varied (Fig. 5a). Therefore, some of the reported changes may have been transient (e.g., Alatalo et al. 2022), whereas other changes may take longer to become apparent because the underlying processes operate over longer time scales. Observed vegetation responses may depend on the amount of perturbation experienced during the study period and on the state of the vegetation at the time of sampling (Lalechère et al. 2025; Saccone & Virtanen 2016; Staude et al. 2023; Stuble et al. 2021). Potential drivers of transient changes in tundra include short-term vole, lemming, and moth peaks (Olofsson et al. 2009, 2013; Siewert & Olofsson 2021) and extreme winter events (Bjerke et al. 2017).

Heterogeneity can also arise when studies that analyze relative changes (e.g., change in relative cover) produce different results than studies that analyze absolute changes (e.g., Study II). While both approaches provide important evidence, different conclusions can be drawn from the same data depending on which approach is used. For instance, when shrubification leads to an increase in total vegetation cover, as was observed in Studies I and II, vegetation trends may diverge between studies because species with stable absolute cover can nevertheless decline in relative cover.

While local variation in vegetation responses to climate change can be high, regional-scale studies can help to identify key trends (e.g., Studies I and II; Bråthen et al. 2024; Tuomi et al. 2024). However, future long-term studies should more explicitly explore spatial scale by incorporating analyses of differing grain sizes and consider how the selected extent can impact the results (e.g., Blowes 2026; Chase et al. 2018; Dornelas et al. 2023; Staude et al. 2023; Valdez et al. 2023). Additionally, community data from local-scale studies (which were numerous in Study III) could be combined for regional-level evidence in Northern Fennoscandia. This approach would better capture the

region's broad environmental gradients and thereby improve assessments of long-term vegetation change. Nonetheless, since observational data are not the primary approach to study drivers of change, the main aim should be to combine large-scale observational and experimental evidence to better understand vegetation responses (e.g., Bjorkman et al. 2020). This strategy would also support future predictions on how vegetation will respond to interacting global change drivers.

The effects of long-term vegetation changes on the ecosystem functioning of Northern Fennoscandia need to be studied next. It is highly likely that crowberry encroachment has shifted heathland and tundra functioning by, for example, altering nutrient cycling (e.g., Stark et al. 2023b) and by decreasing the pasture quality of semi-domesticated reindeer (Tuomi et al. 2024). Moreover, it can affect carbon exchange between soil and atmosphere (e.g., Parker et al. 2021). These changes may not only affect plant community dynamics and plant-animal interactions but also directly harm the livelihoods of the indigenous Sámi people (Markkula et al. 2019) and hinder climate change mitigation and adaptation. Similar to Study II, existing community-level data can be combined with available trait data (e.g., Niittynen et al. 2026; Tyler et al. 2021) for species found in Northern Fennoscandia to gain insight into changing plant functional composition. Nevertheless, if research aims for a comprehensive understanding of long-term change and its drivers, we should not forget to simultaneously consider underlying changes in species identity and abundance.

Considering these factors would not only advance scientific knowledge but also improve the monitoring, conservation, and management of ecosystems. Long-term data and studies are crucial for revealing what changes have already occurred—and their magnitude and direction— and identifying which species and habitats are most at risk. Monitoring programs and assessments from the national to the global level (e.g., Kontula & Raunio 2019; Moersberger et al. 2024; IPBES 2019) would benefit from a wider scientific basis for long-term changes to set valid baselines, estimate the magnitude and direction of change and the risk faced by species and habitats, and assess where interventions (e.g., conservation or restoration) should be implemented.

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