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Abstract

Intensive forest management has led to forest homogenization with associated changes to biodiversity. Compensatory actions have been taken to counteract the negative effects of these practices on biodiversity, but the effectiveness of these actions depends both on which scale they are evaluated and the group of species they are addressed to. In Sweden, the state-owned forest company Sveaskog has developed landscape restoration projects called ecoparks to create multipurpose forests which combine production, recreation and enhancement of natural values. Previously, little research has been done on wild bee communities (Hymenoptera: Anthophila) in boreal forests. With a functional and multi-scale approach, this study aims to figure out whether and how different management regimes affect diversity patterns of wild bee communities. The study also investigates if there are differences in species and functional composition between these management regimes. A pair of landscapes consisting of an ecopark and a conventionally managed production landscape were selected in the south and north of Sweden. Bees were sampled during three years in open and sun-exposed plots where local environmental variables were measured. The percentage of open areas surrounding each plot at different scales was also extracted. Results showed no differences in diversity patterns nor in composition or functionality of wild bee communities between management regimes. Instead, there were differences (except in functional composition) between southern and northern regions. There was higher alpha diversity in the north and higher gamma diversity in the south. The northern region had a higher local functional diversity than the southern one. Functional diversity was, in general, positively related to deadwood diversity but when analysing the data by regions, just the southern one was significantly related to deadwood diversity. The latter relationship might be explained by the diversity of the dataset in terms of species functionality. Despite the little time elapsed since the beginning of restoration, this study suggests that landscape could be playing an important role in the assemble of wild bee communities and highlights the potential of using a functional approach when assessing the effects of different management regimes on wild bee communities.

Keywords: wild bees, Anthophila, forest management, functional diversity, inventory diversity, landscape ecology, boreal forest

Preface

After a whole summer doing fieldwork and looking for the longhorn beetle *Tragosoma depsarium* without any success, a change of topic for the thesis, and a whole year of ups and downs, here there is the culmination of the two years of the master programme in Management of Fish and Wildlife Populations in the Swedish University of Agricultural Sciences in Umeå. Working in the restoration ecology group at the at the department of Wildlife, Fish and Environmental Studies has been a very enriching experience. It has been a pleasure to be part of it for a while.

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1. Introduction

Since the beginning of intensive forestry in Fennoscandia in the nineteenth century, different actions have been taken to increase the effectiveness of silvicultural practices. Consequently, it has had direct effects on the natural succession cycle of the forest and, therefore, on its structural composition and biodiversity (Koivula and Vanha-Majamaa 2020). In Sweden, before even-managed and clear-cutting harvesting models were introduced, boreal landscapes were dominated by fire-affected uneven-aged Scots pine stands which made up more heterogenous forests (Berglund and Kuuluvainen 2021). Nowadays, more than 90% of production forests are structurally simplified (Gustafsson *et al*. 2010, Koivula and Vanha-Majamaa 2020). While just a few species are benefited by modern forestry, more than 50% of the Fennoscandian red-listed species try to thrive in forest habitat and are mainly threatened by intensive forest management (Henriksen and Hilmo 2015, Hyvärinen *et al*. 2019, ArtDatabanken 2020). On the other hand, policies have been implemented on sustainable management of forests which aim to preserve the biodiversity they harbour and the ecosystem services they provide (Forest Europe 2015, The Montréal Process 2015, DG Environment 2017, IPBES 2019). To maintain a favourable conservation status and counteract the negative effects of modern forestry, actions have been taken. For example, since fires are one of the most significant natural disturbance agents within boreal forests (Gauthier *et al*. 2015, Gustafsson *et al*. 2019), prescribed burnings are used to emulate the processes that forests would get through under natural fires events (Vanha-Majamaa *et al*. 2007, Hekkala *et al*. 2014). Furthermore, due to high number of deadwood dependent species in boreal forests, stumps and fallen trees are also saved, and deadwood is artificially created (Abrahamsson and Lindbladh 2006, Hjältén *et al*. 2010, Halme *et al*. 2013, Hekkala *et al*. 2016). Another practice used to offset the effect of clear-cutting is the retention of whole stands of living trees, which may improve connectivity between the fragmented landscape and act as “lifeboats” for forest species (Rosenvald and Lõhmus 2008, Jonsson and Siitonen 2012, Gustafsson *et al*. 2020).

When determining the effectiveness of these management actions, the research focus has been on several species groups like ground-dwelling arthropods and saproxylic beetles (Hyvärinen *et al*. 2009, Matveinen-Huju *et al*. 2009, Djupström e*t al*. 2012, Heikkala e*t al*. 2016, Hjältén *et al*. 2017, Hägglund and Hjältén 2018, Jonsell *et al*. 2019), understory vegetation (Perhans *et al*. 2009, Hautala *et al*. 2011, Rodríguez and Kouki 2015, Granath *et al*. 2018) or fungi (Penttilä *et al*. 2013, Suominen *et al*. 2018, Pasanen et al. 2019). However, in comparison, little is known about how modern forestry and restoration measures affect the order Hymenoptera and particularly wild bees (Anthophila clade). Wild bees are main pollinators and some species rely on the access to deadwood as this is the place where they nest in (Westerfelt *et al.* 2015, Carper and Bowers 2017). According to Proctor *et al.* (2012), homogenization of the forest due to monoculture management or suppression of fires can lead to a reduction of the understory plant diversity and, therefore, to a decline of insect pollinators. Additionally, the reduction of viable wood-nesting structures and soil compaction may also have a negative impact (Romey *et al.* 2007). On the other hand, clear-cutting creates canopy gaps that allow greater light penetration, which is associated with a greater understory plant abundance and species richness. This leads to an increase in floral resources and positively affects pollinators (Quintero *et al.* 2010, Rodríguez and Kouki 2017). Additionally, it is known that wildfires play an essential role in bee composition (Potts *et al.* 2003, 2005, Campbell *et al.* 2007, Grundel *et al.* 2010). Rodríguez and Kouki (2015) showed that prescribed fires have a positive effect on solitary bees' abundance and, consequently, on the ecosystem services they provide.

It is also necessary to take into account that these management regimes may have different effects on wild bee communities regarding the scale at which they are evaluated (Rubene *et al.* 2015b, 2017, Ranius *et al.* 2019). To get a broader picture of the situation it is important to carry out the evaluation at multiple spatial scales, studying not only local habitat variables of forest stands but also the characteristics of the surrounding landscape (Hatfield and LeBuhn 2007, Bergman *et al.* 2012). In Sweden, for example, the state-owned forest company Sveaskog developed the concept of ecoparks. They are landscape restoration projects where different kinds of restoration actions are planned and others are already carried out to improve the forest landscapes and support core areas with known high values for biodiversity.

According to Arena *et al.* (2018), landscape composition is another key piece of the puzzle that determines abundance and species richness of bees in local patches. Changes at landscape scale can have different effects on wild bee communities depending on their specific traits (Hopfenmüller *et al.* 2014). Traits are any characteristics of a species that can be measured and are classified into response traits and effect traits. While response traits allow the species to cope with a particular biotic or abiotic stress - "*to be able to survive, grow and reproduce under the experienced stress level or under different environmental conditions*" (p. 12) -, effect traits are those which somehow affect other species (or individuals) or ecological processes (de Bello *et al.* 2021). Response traits are considered functional traits when they affect the fitness of the species (i.e., all functional traits are response traits but not all response traits can be considered functional traits). Furthermore, not all functional traits affect other species or ecosystem functioning, so not all response traits are effect traits, and vice versa (de Bello *et al.* 2021). Functional traits are any characteristics of the species which directly affect its performance and fitness (Mouillot *et al.* 2013) and are likely one of the factors affecting the species sensitivity to environmental changes (Williams *et al*. 2010). Indeed, assuming that each species affects the functioning of the ecosystem differently due to the sum of their specific traits, it seems quite logical to use functional diversity when working in community ecology. That is because it takes into account the species-specific traits that other measures like species diversity do not (Ricotta and Moretti 2011, Naeem *et al*. 2012). There is not a unique accepted definition of functional diversity, but it could be summarized as the set of species and the expression variation of their traits which somehow influence ecosystem processes (Tilman 2001, Villéger *et al*. 2008, Naeem *et al*. 2012). Therefore, functional diversity is an interesting tool when investigating possible changes in species and functional composition within and between communities after disturbances, and when determining how biodiversity itself can affect ecosystem functions (Mouillot *et al*. 2013, Laureto *et al*. 2015). Additionally, functional diversity is of high interest between ecologists, with several indices being proposed to measure it, such as Rao's Quadratic entropy or Functional dispersion (Botta-Dukát 2005, Petchey and Gaston 2006, Villéger *et al*. 2008, Laliberte and Legendre 2010). There are also several ways to measure diversity, being the concepts of *alpha* (α), *gamma* (γ) and *beta* (β) diversity introduced by Whittaker (1960) some of the most influential ones. While beta diversity itself measures variation in species composition between samples, both alpha and gamma diversity measures diversity at different scales. Alpha diversity measures species diversity within a single sample (local diversity) and gamma diversity measures diversity within a set of samples (total diversity). According to Jurasinski *et al*. (2008), alpha and gamma diversity can be grouped under the term inventory diversity. Gamma diversity can be obtained by the sum of alpha and beta diversity (Jurasinski *et al.* 2008).

Maintaining the functional diversity of bee communities can help to preserve the provision of different types of ecosystem services like pollination (Hoehn *et al.* 2008, Albrecht *et al.* 2012), and strengthen the stability of communities in the face of possible disturbances (Mori *et al.* 2013). Changes in the environment can affect species assemblages, functional composition and diversity and, consequently, have an impact on the functions that these species were providing (Williams *et al.* 2010). Most of the literature about disturbance effects and functional traits on wild bee communities is focused on agricultural landscapes (Forrest *et al.* 2015, Persson *et al.* 2015, Pisanty and Mandelik 2015, Blitzer *et al.* 2016, Bartomeus *et al.* 2018), but little research has been done on the effects of boreal forest management in Fennoscandia.

Therefore, to further investigate the possible effects of local and landscape scale management on the functionality and diversity of wild bees, I will use Sveaskog's ecoparks and conventional production forests as a study system. The concept of ecopark was introduced by the Swedish state forest company Sveaskog Co., among the 4.4 million ha (18% of total forest land in Sweden) of forest they own. Ecoparks are multipurpose forests with the aim to combine production, conservation and human recreation, and today, they consist of 170 000 ha of forest landscapes divided into 37 ecoparks across Sweden. Restoration of natural structures plays a great role in ecoparks' management plans (Angelstam and Bergman 2004, Larsson Ekström *et al*. 2021). The production landscapes are production forests where conventional forestry highly dominates.

This study aims to I) determine whether and how different management regimes (ecoparks vs. production landscapes) affect diversity patterns of wild bees and II) find out if functional and species composition of wild bee communities differ between ecoparks and their respective reference areas.

I hypothesize that I) ecoparks and production landscapes differ in wild bee diversity patterns due to their different management regimes; I expect higher inventory and functional diversity in ecoparks due to less intensive forestry, more protected areas and higher amount of natural values, II) ecoparks have a higher beta diversity and hold different bee community assemblages than production landscapes, and III) inventory and functional diversity have positive relationships with volume and diversity of deadwood.

2. Materials and methods

2.1. Study areas

This study was carried out in two ecoparks and two commercially managed production landscapes in Sweden owned by the state forest company Sveaskog. Each ecopark makes up a study pair with a nearby production landscape similar in composition. The northern pair is located in the central boreal zone, in the region of Västerbotten, and it is made up by Käringberget ecopark and its respective production landscape in Vindeln. Hornsö ecopark and its respective production landscape in Hälleskog in the hemiboreal zone, region of Kalmar, were chosen as study areas in southern Sweden (Figure 1).

Käringberget ecopark was created in 2005 and it is dominated by Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst) with some presence of birch (*Betula pubescens* Ehrh., and *Betula pendula* Roth.) and aspen (*Populus tremula* L.). When it was created, 14% of its area was composed of habitats with high nature values, percentage which is expected to be increased up to 45% after all restoration actions are carried out. Furthermore, its percentage of production forest is planned to be reduced from 86% to 55% (Sveaskog 2005). On the other hand, Hornsö ecopark was established in 2004. It is a fire-influenced forest mainly dominated by Scots pine, together with pedunculate oaks (*Quercus robur* L.), beech (*Fagus sylvatica* L.) and aspen. Two of the goals that are expected to be achieved are to increase the percentage of forests with high nature values from 16% up to 51%, and to reduce the percentage of production forest from 84% to 51% (Sveaskog 2008).

Ecoparks and production landscapes are managed under different regimes and the main differences between them are the proportion of production forests[1] and conservation concern areas[2] (see Appendix 7 to have a bigger picture of the target classes used by Sveaskog). Within these forests of conservation concern are protected areas[3], set-aside forests[4] and a majority of areas where restoration of natural values or structures is being carried out (Table 1). Ecoparks also have greater proportion of forests in higher age classes (Appendix 8).

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[1] Forests where forestry activity mainly takes place.

[2] Productive forests exempted from forestry activity.

[3] Productive forests protected by law for nature conservation.

[4] Productive forests voluntarily protected for nature conservation.

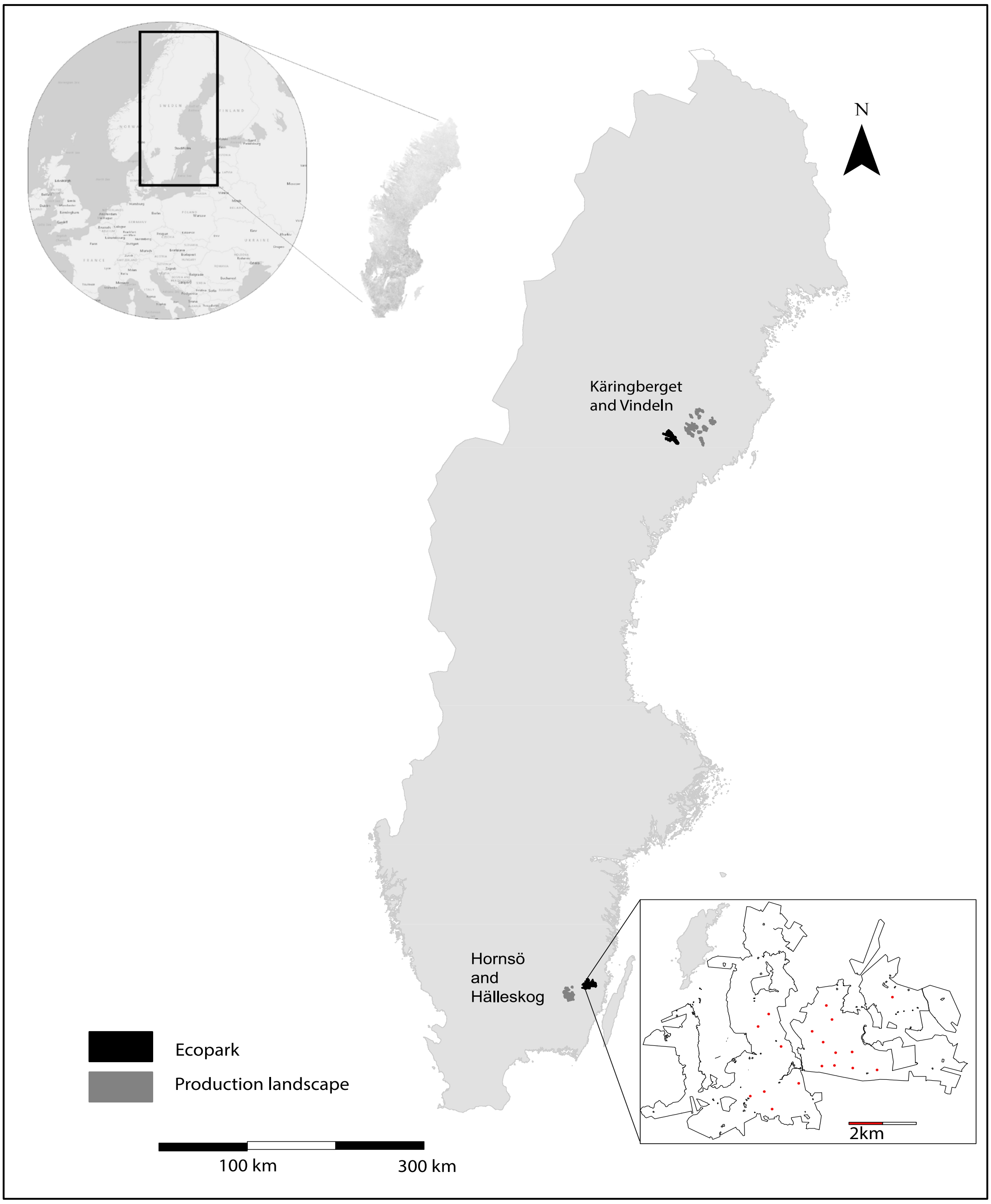

Figure 1. Map of Sweden with the location of northern (Käringberget ecopark and Vindeln production landscape) and southern (Hornsö ecopark and Hälleskog production landscape) study areas, and an example of the distribution of study plots within a study area.

Table 1. Location, size, area distribution and main vegetation type for each study area. ECO = ecopark

Area	Northern Sweden		Southern Sweden	
Management	ECO	Production	ECO	Production
Site	Käringberget	Vindeln	Hornsö	Hälleskog
Coordinates	64° 04' N, 18° 41' E	64° 03' N, 18° 43' E	57° 00' N, 16° 09' E	56° 50' N, 15° 39' E
Size (ha)	13963	21181	9242	9144
Production	5786 (54%)	20066 (95%)	4438 (53%)	8570 (94%)
Conservation concern	4989 (46%)	1115 (5%)	4014 (47%)	574 (6%)
- Restoration	2817 (26%)	18 (0%)	3227 (38%)	124 (1%)
- Set-aside	1615 (15%)	331 (2%)	485 (6%)	381 (4%)
- Protected	557 (5%)	766 (4%)	302 (4%)	69 (1%)
Dominating Vegetation	VT (38%) MT (27%)	VT (46%) MT (27%)	CT (38%) MT (35%)	CT (46%) MT (12%)

VT = Vaccinum type; MT = Myrtillus type; CT = Calluna type

2.2. Study object: wild bees (Hymenoptera: Anthophila)

Hymenoptera is the third most diverse insect order, hosts lots of wood-nesting species and has both a noteworthy role in the ecosystem and a significant socioeconomic importance (Siitonen and Jonsson 2012, Peters *et al*. 2017). Despite the fact that the honeybee (*Apis mellifera* Linnaeus, 1758) is probably the most acknowledged hymenopteran species among the public, the Anthophila clade (bees) consists of lots of wild bee species -of which some might be better pollinators than honeybees (Klein *et al*. 2007)- with singular foraging and nesting strategies. For example, the above-ground nesting bees can dig their galleries directly in living or dead wood, take advantage of tunnels previously created by other insects, or even use human-made structures like bird boxes (Siitonen and Jonsson 2012). Furthermore, they can also nest underground, like some bees of the Halictidae or Apidae family (Michener 2007). Additionally, while the majority of them are generalist (polylectic) or specialist (oligolectic) pollen collectors, there are other species which do not actively gather pollen but parasite the nests of other species so their larva can grow feeding on the harvest of their host (Michener 2007, Dötterl and Vereecken 2010).

Wild bees play a significant role in boreal forest ecosystem. For example, they are the main pollinators of bilberry (*Vaccinium myrtillus* L.) and lingonberry (*V. vitis-idaea* L.) (Rodríguez and Kouki 2015), which are not only important socioeconomic resources for us humans (Pouta *et al*. 2006) but also necessary for some iconic species such as the western capercaillie (*Tetrao urogallus* Linnaeus, 1758) (Lakka and Kouki 2009) or the brown bear (*Ursus arctos* Linnaeus, 1758) (Hertel *et al*. 2016).

However, despite the wild bee diversity in terms of taxonomy, functionality and services they provide to the ecosystem, they have been overlooked in Fennoscandian forest ecosystem research. Therefore, wild bees were selected as study object to contribute to increasing the knowledge of the species in this forest ecosystem.

2.2.1. Functional traits

For the species of wild bees (Hymenoptera: Anthophila) that were found in the study, eight functional traits were compiled (Table 2). These traits likely affect the presence of the species in the areas and could be useful to explain changes in diversity patterns. They are all response traits and considered functional traits because they somehow affect the fitness of the species. They can also be effect traits depending on the question under they are evaluated (de Bello *et al*. 2021). For example, regarding pollination, the functional traits tongue length and diet specialization are also effect traits because they have a direct effect on the pollination of different plant species.

Table 2. Functional traits used in the analyses with a description of the effect the trait has on species functionality.

Trait	Trait type	Levels	Description
Inter tegular distance (mm)	Continuous	N/A	Distance between the wing-attachment bases on the thorax (ITD), related to foraging range (Kendall *et al.* 2019).
Tongue length (mm)	Continuous	N/A	Total length of the tongue, which mediates several characteristics of bee ecology, such as flower choice and plant specialization (Cariveau *et al.* 2016).
Body mass (mg)	Continuous	N/A	It is related to ITD, body size and therefore to foraging range (Greenleaf *et al.* 2007, Cariveau *et al.* 2016).
Nesting behaviour	Categorical	Below-ground nesters Above-ground nesters	Bees can use different substrates (e.g., sand, logs, holes in dead and living trees, abandoned rodent nests, artificial elements like roofs or bird boxes, etc.) to nest under or below the ground (Løken 1973).
Diet specialization		Polylectic (pollen generalists) Oligolectic (pollen specialists)	Bees can visit several families of plants to collect pollen (generalists) or collect it just from a family or even specific species (specialists).
Sociality	Categorical	Solitary Social Eusocial	Bees can socially organise themselves in colonies with division of tasks (eusociality) or live as solitary individuals.
Pollen transportation	Categorical	Tibial corbicula Femoral corbicula Abdominal corbicula Crop Kleptoparasitism	Pollen transportation can be done by specific pollen collecting structures (corbiculae) made up by a set of setae or directly but less frequent via mouth storage (crop). Kleptoparasite bees do not actively collect pollen but steal it from their hosts (Michener 1999).

Trait	Trait type	Levels	Description
Hairiness index	Continuous	N/A	Bee sensory hairs are used to detect electromagnetic fields emitted by flowers and it is shown to be highly related to pollination (Stavert *et al.* 2016, Sutton *et al.* 2016, Zakon 2016).

All traits except for the tongue length and body mass were extracted from literature (Løken 1973, Sydenham *et al.* 2015, Kendall *et al.* 2019, Woodcock *et al.* 2019), the online databases traitbase (Traitbase 2021), bwars (BWARS 2021) and artfakta (Artdatabanken 2021a), and the book "The bees of the world" (Michener 2007). Tongue length and body mass were calculated in R version 4.0.2 (R Core Team 2020) with the BeeIT package (Cariveau *et al*. 2016). Nomenclature of bees follows the online Swedish database Dyntaxa (Dyntaxa 2021). A table with the specific traits of each species can be found in Appendix 1.

2.3. Experimental design

In each ecopark and production landscape, 26 plots representative to the area and accessible from the road were selected (See Appendix 7 and 8 to have a bigger picture of the landscapes). The distance between plots was at minimum 1000 m to avoid spatial correlation, and the plots were thus considered as independent sampling units. Within each plot, a pair of pine and birch high stumps (height 2.5 m, and diameter 15-25 cm) was created in 2010 and 2011 respectively for northern and southern Sweden. The stumps were exposed to sunlight from south and west. In some cases, trees of correct species and/or size were not close enough to each other (1-5 meters), so pairs of two pines or two birches were chosen instead. These were afterwards removed from the analyses of this study.

2.4. Data collection

2.4.1. Sampling of bees

Bees were passively sampled with two flight-intercept traps per high stump. The traps were attached to the trunk at 1.1 and 1.6 meters from the ground and consisted of a 0.5 litres aluminium mould below a 10x20 cm transparent plexiglass sheet. For preserving insects, a 60 percent liquid dilution of propylene glycol with a little amount of soap was used. Traps were set at the end of May and removed at the end of July and were emptied two times per sampling period for 3 consecutive years:

from 2010 to 2012 in the north and from 2011 to 2013 in the south of Sweden. Then, bees were identified by an expert taxonomist (Niklas Johansson, ArtDatabanken, SLU) to species level and separated by stump and year.

2.4.2. Environmental data

Stand scale measurements

In 2019, tree stand structure data was measured at each sampling plot within a 20-meters radius circle which was centred at the middle of the pair of stumps.

Living tree species and their diameter at breast height (DBH, ca 1.3 m) were recorded when the tree height and its DBH were greater than 1.3 m and 4.5 cm respectively. The species, height, DBH and decay class were recorded for standing dead trees and snags. In addition, the maximum and minimum diameters and the length were also recorded for lying dead trees over 1.3m in length and 4.5cm in diameter. The type of dead wood (i.e., standing dead tree, snag, or log) was also recorded.

Decomposition stage of standing trees and snags was classified according to Thomas *et al.* (1979) and Jung *et al.* (1999), while adjusted classification from Gibb *et al.* (2005) was used for deadwood logs. Four decay classes were used for the latter one: 1) hard wood with more than 50% of bark, 2) hard wood with less than 50% of bark and surface beginning to soften, 3) soft wood surface free of bark, with holes and crevices, 4) soft wood, difficult to define surface and outline, possible remaining hard core. Broadleaf trees in advanced decomposition stages were classified as 3 or 4 decay class according to wood softness and regardless of the bark cover percentage. The canopy cover was measured in order to calculate the gap fraction, which is the proportion of sky measured in any direction of the canopy not obstructed by canopy structure (Gonsamo *et al.* 2010). To get that, a fish-eye lens was used to take hemispherical pictures which were later processed in Image J (Schneider *et al.* 2012) with the plugin Hemispherical 2.0 (Beckschäfer 2015). Furthermore, the vegetation type of each site was recorded using the vegetation classification of Cajander (Cajander 1926).

Landscapes scale measurements

Besides these measures, the percentage of open area surrounding each plot at different scales (100- and 500-meters radius circular buffer zones) was extracted from Sveaskog's database of forest structure in 2013 using the software ArcGIS version 10.6 (Esri Inc 2020). Open areas were defined as forests without canopy cover, leaving lakes and mires out of this consideration. To get them, clear-cuts less than 15 years old were chosen. This variable was selected because it was assumed that these areas were open and sun exposed habitats, and therefore beneficial for wild bees due to a greater availability of floral resources and nesting sites (Steffan-Dewenter and Tscharntke 2000, Romey *et al.* 2007, Sydenham, Moe, *et al.* 2016).

2.5. Calculations

Both deadwood and living trees were classified into diameter classes of 10 cm, resulting in six diameter classes (from 4.9 up to > 50 cm). Diversity index of deadwood and living trees per plot was calculated using modified formulas from Siitonen *et al.* (2000) and Hekkala *et al.* (2016). Living tree diversity was calculated as the different combinations of tree species and diameter class. Deadwood diversity index was the number of different combinations of tree species, diameter class, decay class and type of dead wood (i.e., log, snag or standing dead tree). Basal area of living trees and deadwood volume per hectare were calculated for each plot. Volume of intact standing dead trees was calculated based on diameter and height, whereas volume of snags, high stumps and logs was calculated with the cylinder formula based on diameter and length/height. Different formulas for pine, spruce and birch were used, using the latter one for all broadleaf trees larger than 6 meters (Brandel 1990). All calculations and formulas were extracted from Larsson Ekström *et al.* (2021).

2.6. Statistical analyses

All bees caught in the four traps per plot along the three years of sampling were pooled for each plot. Only plots with pine and birch stump pairs were selected, ending up with 20-25 plots per area (Table 3). All the analyses were carried out in R version 4.0.2 (R Core Team 2020).

Different measures of alpha diversity (abundance, species richness and Shannon diversity index per plot) were calculated using the packages plyr (Wickham 2011), doBy (Søren and Halekoh 2020) and vegan (Oksanen *et al.* 2020). To compare total diversity (gamma diversity) among regions and between management regimes within regions while exploring if the current species richness values were skewed due to a small sample size, rarefaction and extrapolation curves of species richness were performed using the iNEXT package (Hsieh *et al.* 2020). Differences between curves were tested following Schenker and Gentleman (2001). Alpha and gamma diversity were grouped under the term “inventory diversity” according to Jurasinski *et al*. (2008).

Functional diversity was measured as the indices functional dispersion (FDis) and Rao’s Quadratic entropy (Rao’s Q) and calculated using the FD package (Laliberte and Legendre 2010). For the diversity indices, plots with zero abundance were dropped from the analyses. Functional composition was assessed as community-level weighted means (CWM), combining species and trait matrices as mean trait values weighted by species abundances (Garnier *et al*. 2004). Before calculating CWM, community composition data was log-chord transformed and then normalised in order to reduce skewness in species distribution and get relative abundances (Legendre and Borcard 2018).

To test whether there were differences in tree stand structures between ecoparks and their respective production landscapes, two-sample Mann-Whitney tests were used. Linear models (LM) and generalised linear models (GLM) with Poisson distribution were used to explore relationships between response and explanatory variables. The models predicting FDis and Rao's Q were fitted after removing the plots where just one individual was present. This decision was made because we felt that the sampling method was biased to lower catches and values of FD indices of these plots were zero, decreasing average FD. LMs were used when fitting Shannon diversity index, FDis and Rao's Q as response variables, whereas GLM were used with abundance and species richness. Abundance was also used as a predictor when fitting species richness as a response variable to test whether effects on species richness are independent from abundance. When fitting GLMs, negative binomial models from MASS package (Venables and Ripley 2002) were used for correcting overdispersion while Poisson models with quasi-likelihood estimation were used for correcting underdispersion.

Akaike weights based on second-order Akaike information criteria for reduced sample size (AICc) between models were compared with the bbmle package (Bolker and R Development Core Team 2020) and those with the lowest ΔAICc values (highest AICc weights) were selected as the best models. Results of the best performing models were extracted with the sjPlot package (Lüdecke 2021) and compiled in Appendix 5.

In order to visualize the species and functional composition of bee communities in the study areas and to have an insight of the differentiation diversity between areas (beta diversity; (Jurasinski *et al.* 2008)), non-metric multidimensional scaling (NMDS) ordinations of species and functional (CWM) composition were plotted using the vegan package (Oksanen *et al.* 2020). Singleton species were dropped before plotting the species composition NMDS to improve convergence. Differentiation diversity, or also called compositional similarity, is one of the two terms that results from the division that Jurasinski *et al*. (2008) make of the concept of beta diversity, and it refers to the variation in species composition between samples.

3. Results

In total, 1466 individuals of 43 different bee species were found. *Andrena lapponica* Zetterstedt, 1838 counts for the 73% of total individuals caught. Most specimens were caught in the northern areas, with 1330 individuals of 23 species. There, *A. lapponica* outnumbers (with 1059 individuals) the rest of species in terms of abundance. It is followed by *Bombus pratorum* (Linnaeus, 1761) (68 individuals), *B. pascuorum* (Scopoli, 1763) and *Hylaeus annulatus* (Linnaeus, 1758) (with 29 individuals each). In the south, the numbers were 136 individuals of 29 species. *Hylaeus communis* Nylander, 1852 was the most abundant species (49 individuals) and it was not found in the northern areas. This species is followed by *A. lapponica* (16 individuals), *H. angustatus* (Schenck, 1861) (8 individuals), and *H. annulatus* (7 individuals). A species list per area can be found in Appendix 2.

A total of 29 species were found in the south and 20 of these were not found in the north. On the other hand, 14 out of the 23 species found in the north were exclusively found in this region (Appendix 3).

3.1. Inventory diversity and functional diversity indices

Significant differences in mean abundance (Wilcoxon rank sum test; $w = 2138.5$, $p < 0.001$), species richness ($w = 1848$, $p < 0.001$), Shannon index ($w = 1341$, $p = 0.040$), Rao's Q ($w = 1757$, $p < 0.001$) and functional dispersion ($w = 1728$, $p < 0.001$) were found between regions, the values being greater in the northern region. However, there were no significant differences between management regimes within regions (Figure 2).

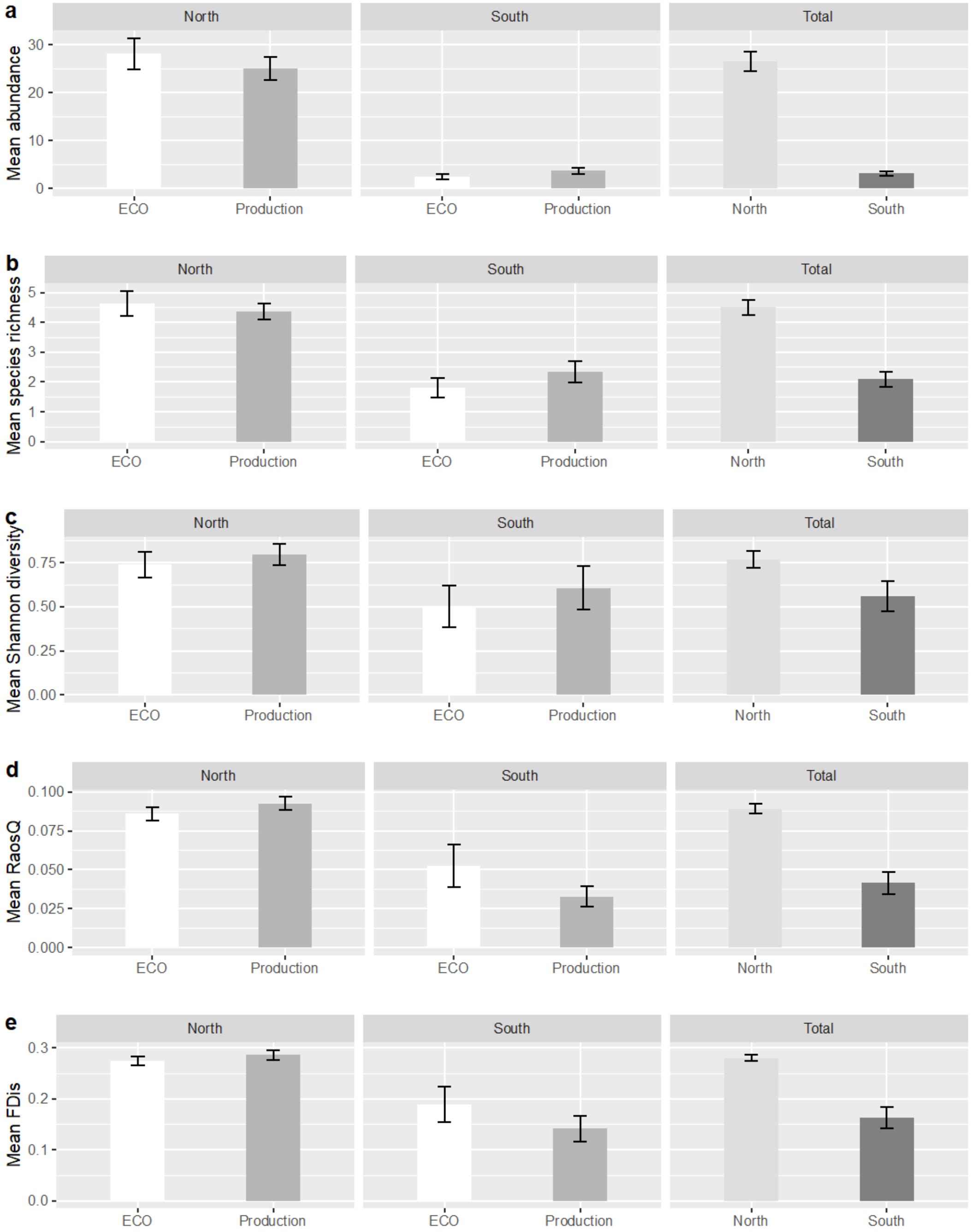

Figure 2. Mean abundance (a), species richness (b), Shannon diversity index (c), Raos' Q (d) and functional dispersion (e) per plot between management regimes within regions and between regions. Whiskers represent ± SE.

When comparing gamma diversity of northern and southern Sweden under equal sample size using rarefaction (Figure 3), it appeared that the southern area had a significantly higher gamma diversity ($z = 2.05$, $p = 0.04$).

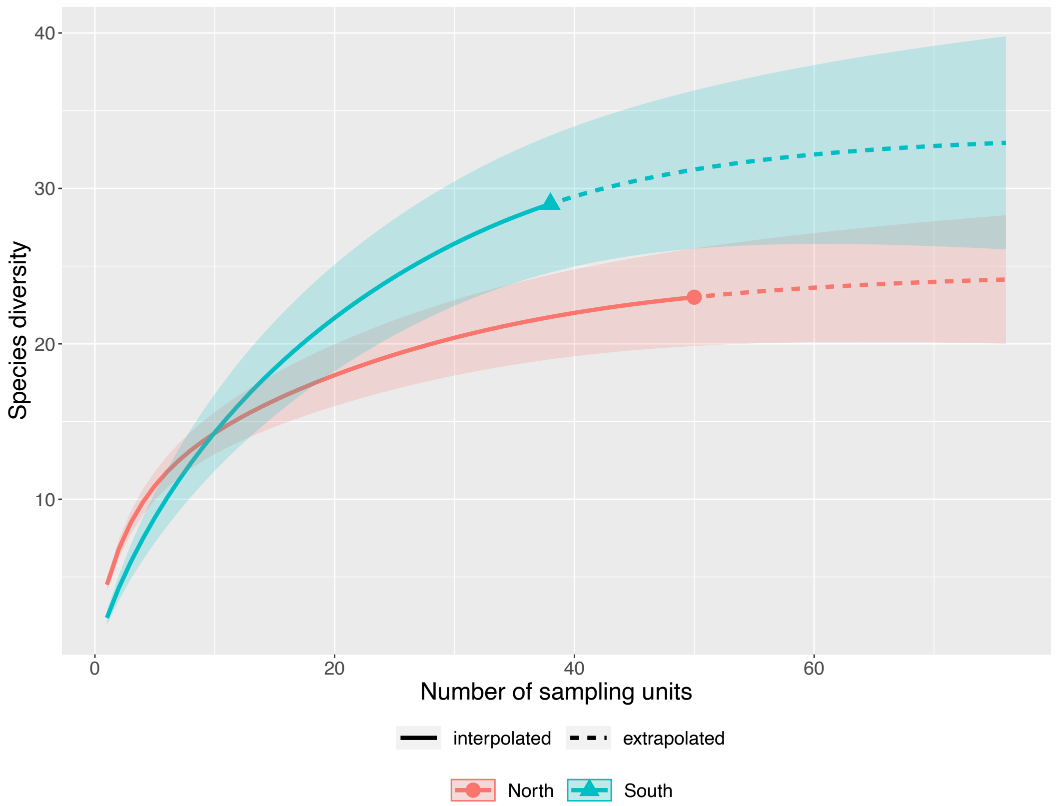

Figure 3. Gamma diversity of northern and southern areas. Sampling units in the north = 50. Sampling units in the south = 38.

No significant differences were found in gamma diversity between management regimes in the north ($z = 1.58$, $p = 0.11$) (Figure 4) or in the south ($z = 0.15$, $p = 0.88$) (Figure 5).

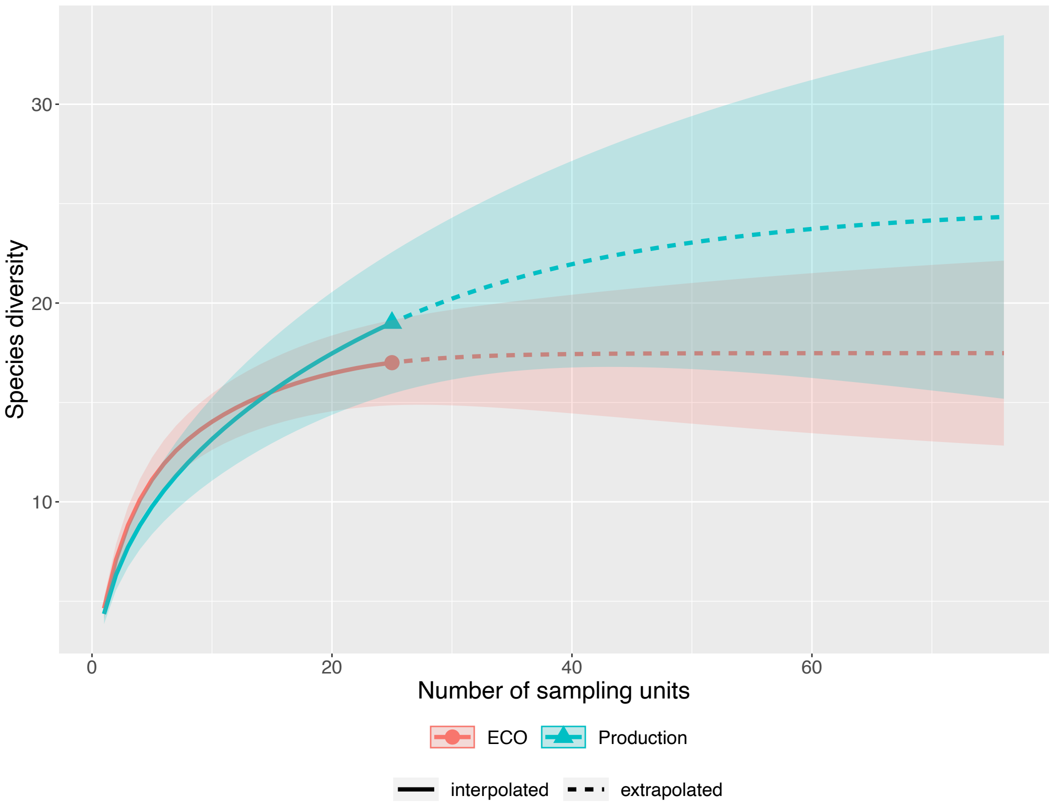

Figure 4. Gamma diversity between management regimes within the northern area. Sampling units in ECO = 25; Sampling units in Production = 25.

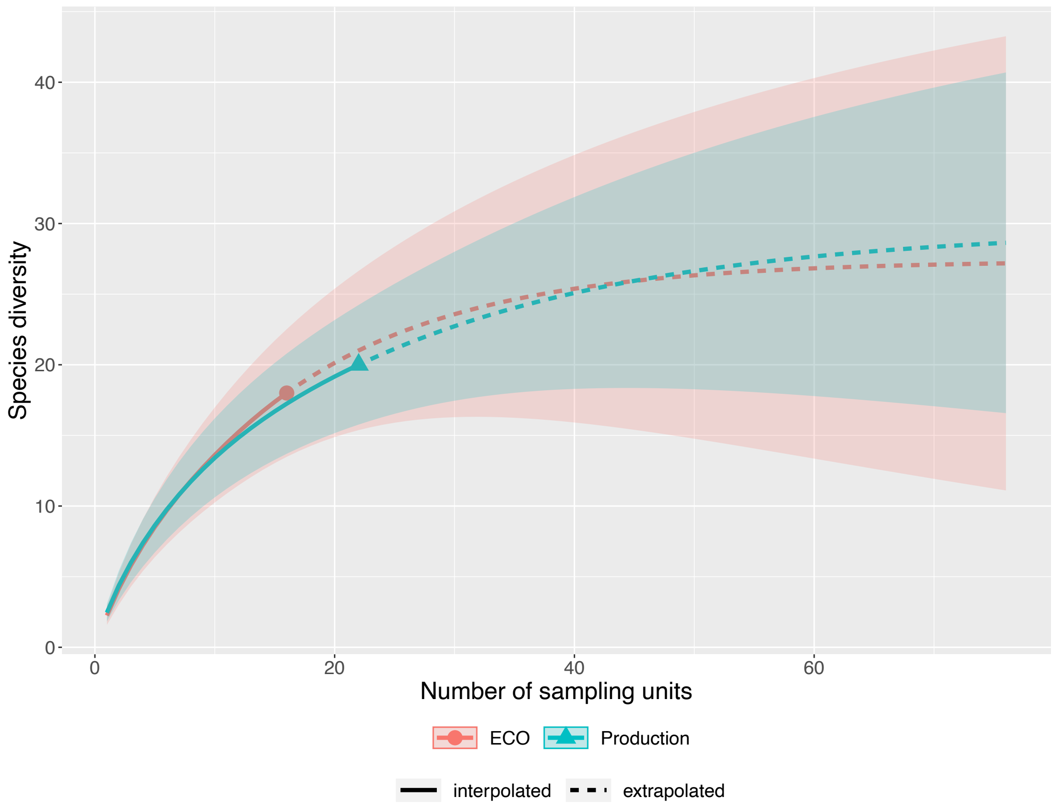

Figure 5. Gamma diversity between management regimes within the southern area. Sampling units in ECO = 16. Sampling units in Production = 22.

3.2. Stand structure data

Basal area of living trees, living tree diversity and deadwood volume were significantly greater in the ecopark than in the production landscape in the south, while there was no difference in deadwood diversity between treatments. In the north, the three first variables were also higher in the ecopark but without significance, and deadwood diversity was significantly higher in the ecopark. Both in the northern and southern areas, the percentage of open areas within a buffer zone of 500 meters was quite similar between treatments. Yet, there were more differences within the 100 meters buffer zone, although they were not significant (Table 3). See Appendix 4 for a summary of stand structure data of each region.

Table 3. Mean±SE values for stand structure data. Highlighted p-values hold statistical significance (p <0.05) based on Mann-Whitney.

	Northern Sweden		p-value	Southern Sweden		p-value
Landscapes	Production	ECO		Production	ECO	
Plots	25	25		22	16	
Basal area of living trees (m2/ha)	10.3±1.5	12.6±1.1	0.160	9.1±1.0	13.9±1.3	**0.023**
Living tree diversity	7.8±0.7	9.2±0.5	0.107	8.1±0.6	12.7±0.8	**<0.001**
Deadwood volume (m3/ha)	6.8±1.2	12.0±2.9	0.065	4.4±0.4	9.1±1.6	**0.002**
Deadwood diversity	7.7±0.8	12.6±1.3	**0.004**	7.1±0.6	9.7±1.2	0.056
Open area % - 500m	6.2±0.9	6.3±1.4	0.711	3.7±0.5	3.3±1.0	0.143
Open area % - 100m	25.1±6.1	14.7±5.1	0.291	8.7±2.3	9.8±3.8	1

3.3. Inventory diversity and functional diversity models

Species richness was positively related to abundance while functional dispersion and Rao's Q had a positive relationship with deadwood diversity (Figure 6). Results in Figure 6 are based on the whole dataset.

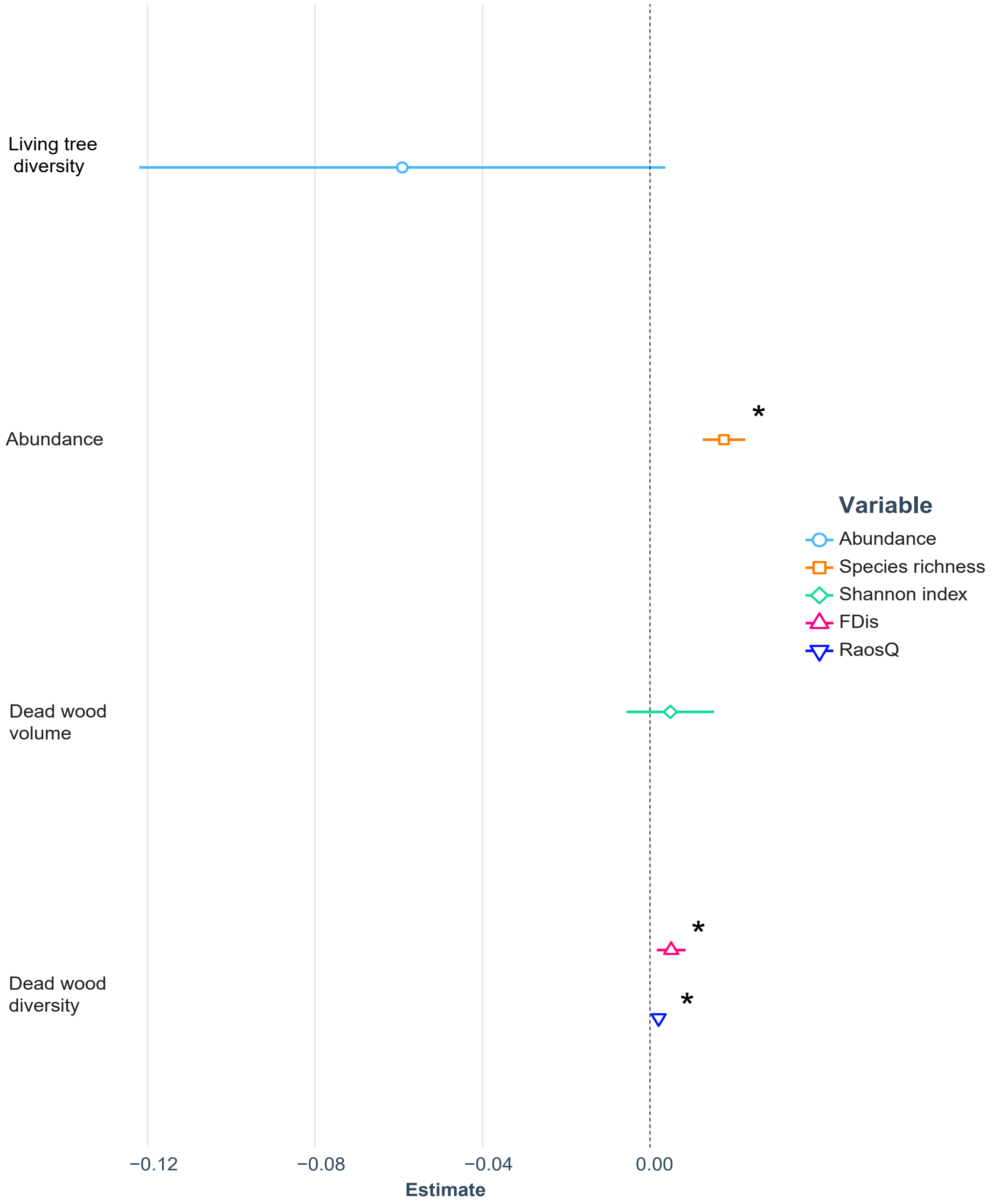

Figure 6. Models for the whole dataset with environmental variables and abundance as predictors. To be significant, estimate±SE must not cross the 0.00 dotted line. The symbol "" indicates significance but not level of significance. Only the best performing models are shown. For more information of the models, Appendix 5.*

Bee abundance in northern and southern landscapes was negatively but not significantly related to the basal area of living trees (Figure 7). In the north, Shannon index, functional dispersion, Rao's Q and species richness were positively related to living tree diversity, being only significant the first relationship (Figure 7a). In the south, functional dispersion had a significant positive relationship with deadwood diversity (Figure 7b).

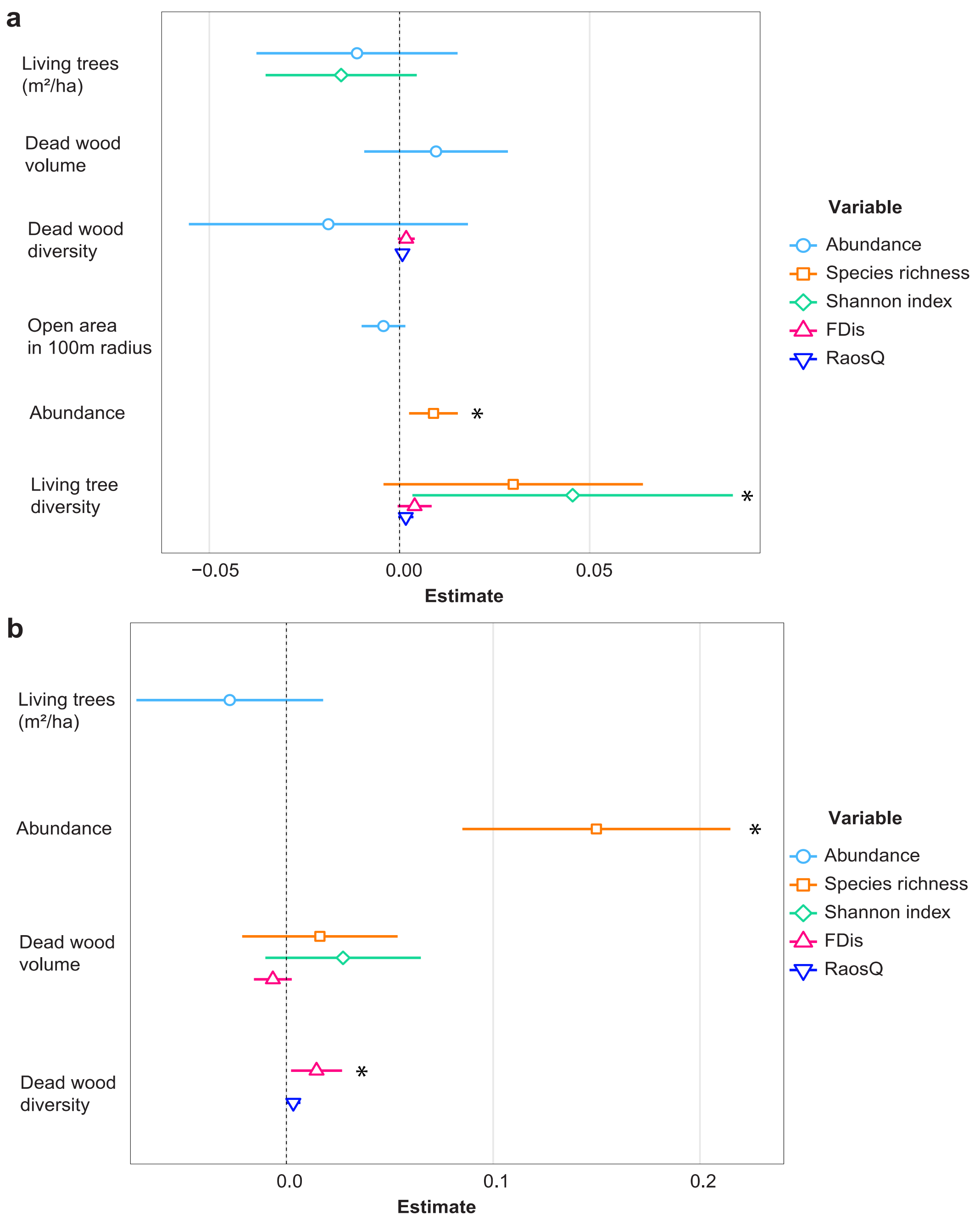

Figure 7. Results of the models plotted by region with environmental variables and abundance as predictors. a) = northern Sweden. b) = southern Sweden. To be significant, estimate±SE must not cross the 0.00 dotted line. The symbol "" indicates significance but not level of significance. Only the best performing models are shown. For more information of the models, Appendix 5.*

3.4. Species and functional composition of bee communities

The species assemblage differs between northern and southern regions, but there are no differences between management regimes in either region (Figure 8). In the north the genus *Bombus* is very well represented, whereas just one species of this genus was found in the south. On the other hand, the genus *Hylaeus* did predominate more in the south than in the north and species of *Chelostoma* genus were only found in the southern areas (see Appendix 6 for a figure with all species shown).

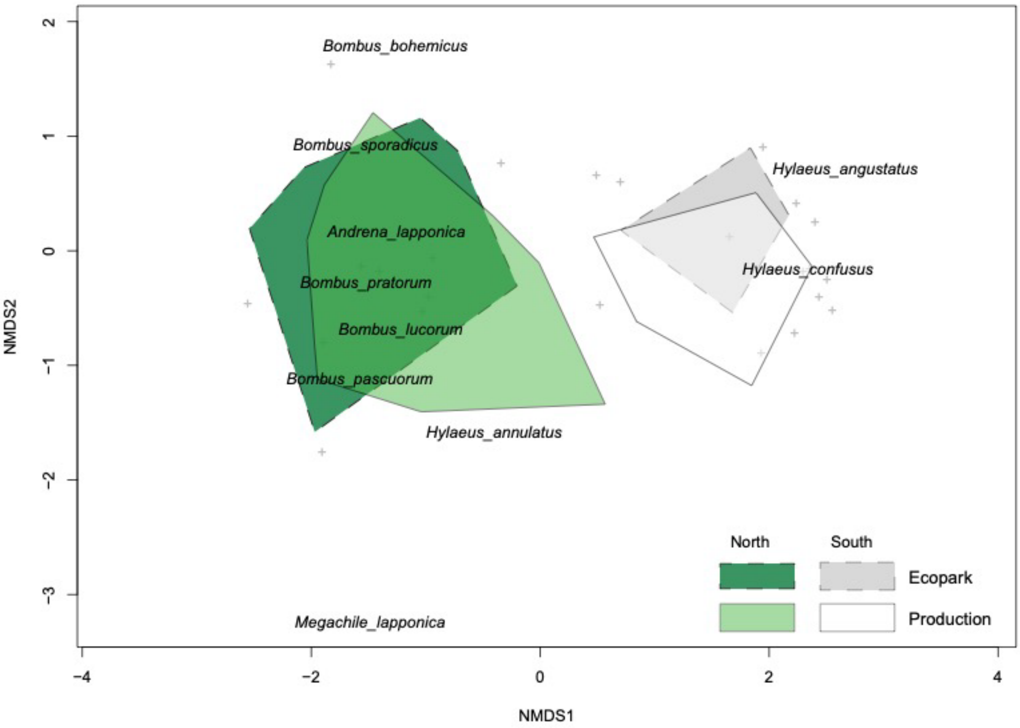

Figure 8. NMDS plot visualizing species composition of study areas. Stress = 0.078. To offer a clear visualization of the plot and avoid superimposition of species labels, only the names of the most abundant ones are shown and "+" symbols replace the rest. See Appendix 6 for a complete figure.

Functional composition in the northern areas was nested within the southern ones (Figure 9). Large and furry bees with a long tongue dominated in the north, while the variation in trait composition among sites was much greater in the south. However, no differences between ecoparks and their respective production

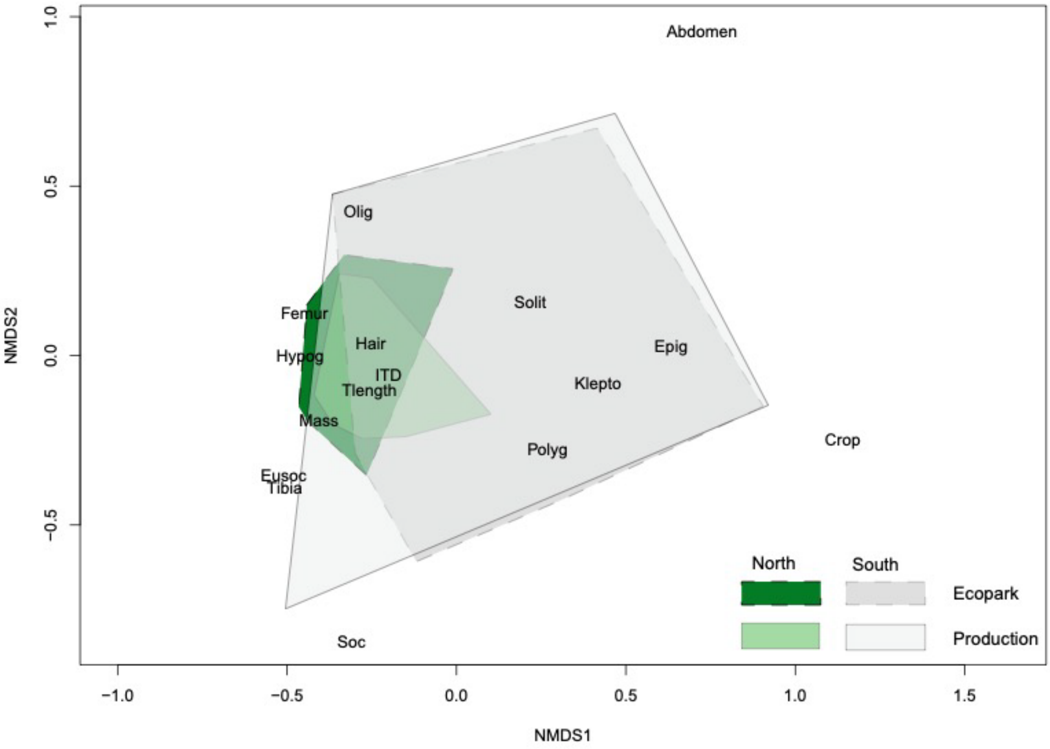

Figure 9. NMDS plot visualizing functional traits composition of study areas. Stress = 0.046. Traits names: Epig = above-ground nesters; Hypog = below-ground nesters; Solit = solitary; Eusoc: eusocial; Soc = social; Olig = oligolectic; polyg = polylectic; Femur = femur crobicula; Crop = crop; Abdomen = abdomen corbicula; Tibia = tibia corbicula; Klepto = kleptoparasitism; Hair = hairiness index; ITD = intertegular distance; Tlength = tongue length; Mass = body mass. See Table 2 for closer explanations.

4. Discussion

4.1. General findings

There were no differences in inventory diversity, species assemblages, functional composition nor functional diversity of wild bee communities between management regimes. Instead, there were differences (except in functional composition) between southern and northern regions.

There was higher alpha diversity in the north and higher gamma diversity in the south, but no greater beta diversity in the south, possibly due to the removal of singletons in the species composition analysis. The northern region had a higher functional diversity than the southern one.

Functional diversity was, in general, positively related to deadwood diversity but when analysing the data by regions, just the southern one was significantly related to deadwood diversity.

4.2. Inventory diversity and functional diversity

4.2.1. Ecoparks versus conventionally managed forest landscapes

Contrary to what was hypothesized, no differences were found in inventory diversity between the two different management regimes. Some similar results were found in Larsson Ekström *et al.* (2021) regarding saproxylic beetles. That study was carried out in the same study areas as this thesis, and they observed no differences in alpha diversity between the landscapes in the north but a greater alpha diversity in the southern ecopark in comparison with the production landscape. Additionally, they showed that there was a greater species richness of red-listed species in both ecoparks than in forest production landscapes, which suggests that conservation-orientated managed landscapes can host more red-listed species than other conventionally managed forests. In contrast, my study does not yield evidence to support that wild bees are positively affected by ecoparks management actions yet, which might be due to the short period of time between the creation of the ecoparks and the sampling of bees. It is necessary to bear in mind that this study is part of a long-term project running from 2009 to 2033, so when bees were sampled, none or very few planned actions to improve the natural values of the landscape had been taken yet. Furthermore, as Granath *et al*. (2018) mention, it is highly unlikely that all targets aimed by the management plans are reached at the same time. Since different goals need different time to be fulfilled, organisms with different ecology, life history and requirements may respond differently to implemented actions.

4.2.2. Southern and northern regions

According to the results, the greater alpha diversity in the north cannot be explained by its greater volume and diversity of deadwood. The analyses did not yield significant relationships between them, but it is worth mentioning that these results may be skewed due to the large number of specimens of *A. lapponica* that were caught, counting for the 80% of all specimens caught in the northern area. This species does not use wood resources because it is a below-ground nester, which could explain that lack of relationship between deadwood and alpha diversity. The greater species richness of bumblebees in colder habitats (Nieto *et al.* 2014) may be positively affecting the greater alpha diversity in the north. Furthermore, from in situ observations it seems that southern forests are much more dense than northern ones and that the understory vegetation of both regions are quite different. While dwarf shrubs (*V. myrtillus*, *V. vitis-idaea*, *Empetrum nigrum* (L.) and *C. vulgaris* dominate in the north, in the south there are some zones with thick *Calluna* carpets, others with some lingonberry present but also areas with scarce understory vegetation (just mosses, some herbs, saplings of beech and oaks or ferns). This is not reflected in the data because of the coarseness of vegetation typing, but it might be affecting the different diversity patterns between regions and could be one of the reasons why barely any bumblebees (*Bombus* spp.) and so few *A. lapponica* were caught in southern landscapes. Another factor which may be influencing the difference in alpha diversity between regions is the foraging pressure of ungulates. Despite current knowledge about the effects of grazing on wild bee communities is still inconclusive, it seems to be dependent on the intensity of grazing (Danforth *et al.* 2019). Thus, a possible greater density of some ungulates like fallow deer *Dama dama* (Linnaeus, 1758) in the southern areas could explain the lower alpha diversity in this region. They may be homogenizing the lower vegetation layer of the forest and, potentially, reducing the flowering of dwarf shrubs. This could negatively affect the presence of some wild bees. This herbivores foraging effect hypothesis concurs and contrasts with some other studies (Vulliamy *et al.* 2006, Hatfield and LeBuhn 2007). Another hypothesis could be that, in the northern region, other and more common ungulates like moose and reindeers may be shaping the lower vegetation layers of the forest creating more open and flower-rich suitable local habitats for wild bees. A suboptimal sampling methodology (i.e., high-situated flight-intercept traps) might also be influencing the incredibly few bees found in the south and therefore affecting the lower alpha diversity in this region.

Gamma diversity was significantly greater in the south than in the north, which is logic due to the biogeographic filtering of bee species in Europe. The highest species richness is found in Southern Europe and declines gradually towards northern latitudes and the northeast of Europe (Nieto *et al.* 2014). Furthermore, the pre-forestry history of southern landscapes could also be influencing gamma diversity in the south. According to Lindborg and Eriksson (2004), the historical composition of the landscape can play an important role on today's diversity patterns, and the study of Ibbe *et al*. (2011) serves as an example. They showed that inventory diversity of butterflies was greater in clear-cuts historically managed as meadows than in clear-cuts which were historically coniferous forests. Furthermore, the study of Milberg *et al.* (2019) in southern Sweden found that forests with a history as meadows were more similar both in species and trait composition of plants to grasslands than forests with a forest history. Thus, it is plausible that these remnants of former pastures and meadows (Dahlström *et al.* 2006) may be positively affecting the current total diversity of bees. This historic influence might be helping to maintain a different landscape composition, perhaps with more diverse floral communities than in the north, which enables a greater number of species to thrive.

This study did not find any significant relationship between the percentage of open areas and the inventory diversity, even though the relationship was expected because wild bee species require floral and nesting resources assumed to be greater in these open habitats than in densely populated forests. Indeed, Rubene *et al.* (2015a) found a significantly positive relationship between species richness of below-ground nesters and the proportion of open areas within 2 km. In our study, the percentage of open areas within 500 m was greater (although not significantly, perhaps due to the zeros present in the dataset) in the northern region than in the southern region (See Appendix 4), which may be a reason why *A. lapponica* was that abundant in the northern areas. This below-ground nesting species might be benefitting from these early-successional habitats by having an adequate substrate to dig their nest in while foraging in the coniferous forest in various plant species of *Vaccinium* like blueberry (*V. myrtillus* L.) and lingonberry (*V. vitis-idaea* L.) (Artdatabanken 2021b).

Functional diversity was, in general, positively related to deadwood diversity, even though it was significantly related to deadwood diversity in the southern region but not in the north. The general relationship between deadwood diversity and FD might be explained by the high correlation (> 0.7) between deadwood diversity and the number of suitable deadwood pieces per hectare (CWD pieces/ha)[5] for nesting bees. It might also have to do with the diverse functional groups of our database, made up of species which nest in deadwood and others which are completely independent of this resource. The significant relationship between functional diversity and deadwood diversity in the south may be justified by the species composition of these areas. There, small-sized and above-ground nesters like some species of *Chelostoma* and *Hylaeus* dominate, which use deadwood to dig their nest in or take advantage of holes already created by saproxylic beetles. However, that relationship was not found in the study of Rubene *et al.* (2015a) in central-south Sweden about wild bees and wasps and argued that it may be caused by the relative fresh stage of deadwood and the few cavities bored by other insects. Sydenham *et al.* (2016) found a positive relationship between wood boring beetles and cavity-nester bees and claimed that it might be an important factor to take into account when investigating wild bee communities assemblages. In our study, the bees were collected during three years after stump creation, after a considerable amount of beetles had inhabited the stumps (Larsson Ekström *et al.* 2021). The intermediate landscape-complexity hypothesis (Tscharntke *et al.* 2012) could also explain why there was not a significant positive relationship between functional diversity of bees and deadwood within the northern areas while there was in southern Sweden. This hypothesis suggests that conservation and restoration efforts would be more effective in intermediate complex systems than complex ones due to the already structural complexity present in the latter ones (Tscharntke *et al.* 2012, Jonsson *et al.* 2015). If one considers the northern landscapes to be more complex because they generally have greater volume of deadwood (Fridman and Walheim 2000), the southern region would be of intermediate complexity because it has been more intensively exploited than the northern one. Then, it would explain the significant relationships between deadwood and diversity of bees in southern landscapes but not in the northern ones.

4.3. Beta diversity and functional composition

Species assemblages did differ between southern and northern regions even though the results do not allow us to see clear differences in β diversity (see size of polygons in species composition NMDS). Since gamma diversity is the sum of local diversity and the variation in species composition among sites, I expected to obtain a higher beta diversity in southern Sweden which could have explained the greater gamma diversity in this area. However, the NMDS ordination of species composition does not show that result. This may have arisen from dropping the

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[5] This variable was calculated after all the results to look for a possible explanation for that relationship. It refers to all logs and snags with a diameter greater than 10 cm and not rotten.

singletons before performing the species composition NMDS, as 7 out of 9 species dropped were present in the south.

Regarding functional composition, the results showed no clear differences between management regimes within regions nor between regions, but southern landscapes showed higher trait variation among sites than northern landscapes. This pattern might arise due to the dominance of *A. lapponica* and bumblebees in the north, the difference in understory vegetation composition between northern and southern landscapes (being more heterogenous among sites in the south at a landscape level) and the management history of the landscapes. Given the long history of forest management in southern Sweden, these landscapes should be more homogenous and therefore the expected functional turnover should be lower than in the north, as previously occurred with ants and saproxylic beetles assemblages in managed forests (Martello *et al.* 2018, Micó *et al.* 2020). However, the results do not support that, which suggests that there are still some important patterns yet to be investigated.

4.4. Management implications

Up to my knowledge, this thesis is one of the first studies that specifically investigates with a multiple scale approach how different forest management regimes may affect diversity patterns of wild bee communities in Fennoscandian boreal forests. Thus, despite the general findings should be taken with caution, this is a big step to begin digging up the direct effects of silvicultural and restoration practices both at local and landscape scale on this taxon. When evaluating which management action should be taken, it is very important to take into consideration the ecology of the species which these actions are addressed to. In this regard, functional traits play an important role and give us interesting insights on the management practices that may benefit different species. Additionally, there are some studies that emphasize the importance of local patch characteristics to predict diversity of invertebrates, but it is also essential to bear in mind that some pollinators can traverse relatively long distances to gather resources such as pollen or nectar. Consequently, landscape characteristics may affect them in a greater way than other insects with smaller foraging and home ranges. Yet, there are also some small-sized bees which can be negatively affected by landscape fragmentation. According to Danforth *et al.* (2019) solitary bees are more prone to suffer low levels of genetic variability due to the reduced gene flow between populations, normally caused by the patchy distribution of their host plants and their small foraging ranges. This may have implications for bee conservation and highlights the importance to focus not only on local level actions but also formulate plans aimed to increase the heterogeneity and connectivity at a landscape level.

Therefore, a better understanding of their habitat requirements both at a local and landscape level, together with a functional group approach, can help to formulate precise and accurate restoration actions which would efficiently protect and maintain the so important wild bee communities of our forests.

4.5. Further investigation

Given that this thesis is the first study within a long-term project and has already found significant results, further analyses of the data could help to clarify some patterns and find robust relationships. For example, by creating functional groups we may dig up more into specific conservation-related questions like: is the above-ground nesters diversity positively related to deadwood diversity and volume of deadwood? If it is not, can it be due to very low floral resources? Is the inventory diversity of small and above-ground nester bees related to the diversity of small saproxylic beetles?

Since the structure of bee communities is very linked to that of floral communities, understanding how floral resources are distributed in the study area is of paramount importance. Thus, a floral inventory may help us to clearly explain different diversity patterns. Furthermore, it might be interesting to have forest roads in mind in next studies since they are normally sun-exposed and constant open habitats which provide both flower resources to gather food from and viable soil type where below-ground nesters can dig their nests in.

It would also be very interesting to repeat the analyses dropping the overrepresented species *A. lapponica* to see if some patterns are clarified or new ones appear.

Some other trapping methodologies (e.g., pan traps, direct observations, sweeping nets, etc.) can be tried to increase the sample completeness and to eliminate the bias which this study's sampling methodology is assumed to have. The database is made up of 49 species and there were 25 solitary bees (out of 37) of which only 5 or less individuals were caught. It is both curious and intriguing the low number of individuals that were trapped during the three years of sampling, and it may be worthwhile to investigate this pattern more deeply and relate it to sampling methodology and landscape connectivity.

Finally, it would be interesting to follow the continuing research between the different management regimes to see if there is a difference in, for example, ten years from now. It would also be interesting to see if the results would show any difference in a comparison of production forests and landscape restoration projects among other companies.

4.6. About the experimental design and the possible pseudoreplicates

Due to the sampling design of this study, one could argue that the sampling plots are pseudoreplicates because the distance between sampling plots is not great enough to consider them as independent samples. Nevertheless, given the geographic scale of the landscapes (>5000 ha) and the scale of the bee's movement, I consider that 1 km distance between sampling plots can be a substantial distance for wild bees and therefore I consider the plots as independent samples when comparing management regimes within regions. According to Hurlbert (1984), this study would have an issue of pseudoreplication in strict sense because the experiment has been restricted to a few plots which can be sampled within a short period, so "*the space over which samples are taken is smaller or more restricted than the inference space implicit in the hypothesis being tested*" (p. 190). Later, Hurlbert (2009) claims that pseudoreplication occurs when "*there is a single experimental unit per treatment, but multiple measurements on each experimental unit . . . These multiple measurements are then treated statistically as if each represented a separate experimental unit*" and also when "*multiple measurements on an experimental unit are taken successively in time and are treated as if each represented a different experimental unit*" (p. 437). However, Hargrove and Pickering (1992) argue that "*classical experiments are not well-suited to regional ecology [...] classical experimentation is most practical to reductionist approach*" (p. 253). Despite replicates are necessary, replication at large scales are difficult and expensive. Due to the general impossibility to experiment in the classical sense at regional scales and durations, Hargrove and Pickering (1992) argue that careful pseudoreplication leading to conclusions could be necessary in these studies: "*Regional ecologists cannot afford to eschew induction and pseudoreplication as inferior; indeed, we must embrace these as primary investigative tools*" (p. 255). Hurlbert (1984) agrees with that statement because replication is often impossible in large scale landscapes or replicates can be very expensive, but adds that the results derived from this unreplicated treatment should be carefully taken when making conclusions.

It is essential to include more ecoparks and production landscapes to obtain a greater statistical power when comparing different management regimes and for further evaluation of the ecopark concept. Yet, besides this is out of the scope of this thesis, each ecopark should be treated as a single study case as each has its own management plan. This study can be considered as a case study with two cases and a comparison between southern and northern regions.

Overall, I think that this study has contributed to increasing the knowledge about wild bees in Swedish boreal forests. However, one can only carefully extrapolate the results of one ecopark to all Sveaskog’s ecoparks in Sweden. Since they are all distributed across the country, the most northern and southern ones can differ in species composition solely due to their geographic position, but that does not mean that one is not as well managed as the other one. To get the best conclusions out of these studies, while bearing in mind the large discrepancy in latitudes within the country, one should pay attention not only to the results of their analyses but also to the possible biodiversity differences inherent to the geographic position of the study landscapes.

5. Conclusion

This study explores the diversity patterns and composition of wild bee communities between two different forest management regimes (organised by the company Sveaskog) and two regions using a functional trait and multiscale approach.

The results of the study show no differences in diversity patterns or composition of wild bee communities between ecoparks and conventionally managed production landscapes. This might be explained by the short time elapsed between the establishment of these ecoparks and the sampling of bees. Conversely, the study of Larsson Ekström *et al.* (2021) conducted in the same study areas found not only greater alpha diversity of saproxylic beetles in the southern ecopark than in its respective production landscape, but also a greater species richness of red-listed species in both ecoparks. These results indicate that wild bee communities respond differently than saproxylic beetles to the same management regimes and suggest that one should not come up with an early conclusion about the effects of these two different management regimes on wild bee communities in Fennoscandian boreal forests.

Differences in diversity patterns and composition of species were found between southern and northern regions. The greater alpha diversity in northern Sweden cannot be explained by its greater amount of deadwood even though this lack of relationship can be skewed due to the overrepresentation of the below-ground nester A. lapponica in this region. Total diversity was greater in the south of Sweden, probably due to the biogeographic differences between regions. The pre-forestry history of southern landscapes might also explain this difference. Lots of current forests were previously managed as meadows, so there can exist remnants of vegetation which help to create a more heterogenous landscape and therefore increase the total diversity of wild bees in southern Sweden (Dahlström *et al.* 2006, Milberg *et al.* 2019). This result enhances the importance of a multiscale approach when planning and evaluating different management regimes.

Functional diversity was positively related to deadwood diversity in the south but not in the north, likely due to the diversity of the database in terms of species functionality.

This thesis has found significant results, but it is still the beginning point of a long-term project. Therefore, there is still a lot of room for improvement, like the use of different sampling methodologies and measurement of other important variables, or the use of additional statistical analyses and a deeper analysis of the database.

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Of course, and as always for the last six years, thanks to my *ADNz* group. I wish you could be here with me today.

Appendix

Appendix 1. Species-specific functional traits

Table 4. Functional traits of the different species

	ITD	Tlength	Mass	NEST	Diet	Social	Transport	Hair
Andrena helvola	2.010	2.072	10.687	Hypo	Poly	Soli	Femur	0.792
Andrena lapponica	2.500	2.555	18.315	Hypo	Olig	Soli	Femur	0.792
Andrena minutula	1.420	1.484	4.532	Hypo	Poly	Soli	Femur	0.792
Bombus bohemicus	3.495	7.081	41.887	Hypo	Poly	Soli	Klept	0.714
Bombus hortorum	5.120	10.216	107.525	Hypo	Poly	Eu	Tibia	0.875
Bombus hypnorum	4.290	8.621	69.479	Epi	Poly	Eu	Tibia	0.917
Bombus jonellus	4.700	9.410	87.042	Epi	Poly	Eu	Tibia	0.875
Bombus lapidarius	4.760	9.525	89.811	Hypo	Poly	Eu	Tibia	0.792
Bombus lucorum	4.050	8.157	60.272	Hypo	Poly	Eu	Tibia	0.875
Bombus pascuorum	4.310	8.659	70.281	Hypo	Poly	Eu	Tibia	0.834
Bombus pratorum	4.060	8.176	60.640	Epi	Poly	Eu	Tibia	0.792
Bombus sporadicus	5.920	11.744	153.883	Hypo	Poly	Eu	Tibia	0.875
Bombus terrestris	5.430	10.809	124.321	Hypo	Poly	Eu	Tibia	0.875
Chelostoma campanularum	1.030	1.924	2.051	Epi	Olig	Soli	Abdomen	0.571
Chelostoma florisomne	1.770	3.235	7.808	Epi	Olig	Soli	Abdomen	0.619
Chelostoma rapunculi	1.660	3.042	6.664	Epi	Olig	Soli	Abdomen	0.571
Halictus rubicundus	1.920	2.581	9.544	Hypo	Poly	Eu	Femur	0.792
Hylaeus angustatus	1.080	0.926	2.306	Epi	Poly	Soli	Crop	0.125
Hylaeus annulatus	1.350	1.147	4.000	Epi	Poly	Soli	Crop	0.125
Hylaeus brevicornis	0.990	0.852	1.860	Epi	Poly	Soli	Crop	0.125
Hylaeus communis	1.240	1.057	3.243	Epi	Poly	Soli	Crop	0.125
Hylaeus confusus	1.500	1.269	5.188	Epi	Poly	Soli	Crop	0.125
Hylaeus gibbus	1.440	1.220	4.691	Epi	Poly	Soli	Crop	0.125
Hylaeus hyalinatus	1.380	1.172	4.223	Epi	Poly	Soli	Crop	0.125
Lasioglossum albipes	1.640	2.219	6.467	Hypo	Poly	Soci	Femur	0.667
Lasioglossum calceatum	1.750	2.362	7.592	Hypo	Poly	Soci	Femur	0.667
Lasioglossum fratellum	1.500	2.037	5.188	Hypo	Poly	Soli	Femur	0.667
Lasioglossum leucopus	1.200	1.644	2.991	Hypo	Poly	Soli	Femur	0.667
Lasioglossum rufitarse	1.400	1.906	4.376	Hypo	Poly	Soli	Femur	0.667
Megachile lapponica	3.110	5.558	31.400	Epi	Poly	Soli	Abdomen	0.709
Megachile versicolor	2.770	4.973	23.593	Epi	Poly	Soli	Abdomen	0.709
Megachile willughbiella	3.540	6.293	43.231	Epi	Poly	Soli	Abdomen	0.709
Nomada glabella	1.640	3.425	6.467	Hypo	Poly	Soli	Klept	0.167
Nomada leucophthalma	1.789	3.723	8.016	Hypo	Poly	Soli	Klept	0.167
Nomada rufipes	1.553	3.250	5.653	Hypo	Poly	Soli	Klept	0.167
Osmia bicornis	2.470	4.455	17.777	Epi	Poly	Soli	Abdomen	0.917

Osmia laticeps	1.935	3.524	9.7296	Epi	Poly	Soli	Abdomen	0.917
Osmia nigriventris	3.300	5.883	36.351	Epi	Poly	Soli	Abdomen	0.917
Osmia parietina	2.100	3.812	11.908	Epi	Poly	Soli	Abdomen	0.917
Osmia uncinata	2.500	4.507	18.315	Epi	Poly	Soli	Abdomen	0.917
Sphecodes crassus	1.263	1.727	3.393	Hypo	Poly	Soli	Klept	0.542
Sphecodes geoffrellus	1.013	1.397	1.968	Hypo	Poly	Soli	Klept	0.542
Stelis ornatula	2.038	3.704	11.059	Epi	Poly	Soli	Klept	0.476

Appendix 2. List of bee species

Table 5. List of species. Total abundance of species per each study area.

	South		North		
	Ecopark	Production landscape	Ecopark	Production landscape	Total
Andrena helvola	0	1	0	0	1
Andrena lapponica	5	11	571	488	1075
Andrena minutula	1	0	0	0	1
Bombus bohemicus	0	0	5	0	5
Bombus hortorum	0	0	2	1	3
Bombus hypnorum	2	0	9	19	30
Bombus jonellus	0	0	8	4	12
Bombus lapidarius	0	0	2	0	2
Bombus lucorum	0	2	22	2	26
Bombus pascuorum	0	0	16	13	29
Bombus pratorum	0	0	22	46	68
Bombus sporadicus	0	0	17	0	17
Bombus terrestris	4	0	0	0	4
Chelostoma campanularum	0	3	0	0	3
Chelostoma florisomne	1	1	0	0	2
Chelostoma rapunculi	6	1	0	0	7
Halictus rubicundus	0	0	6	4	10
Hylaeus angustatus	4	4	0	0	8
Hylaeus annulatus	1	6	7	22	36
Hylaeus brevicornis	0	6	0	0	6
Hylaeus communis	15	34	0	0	49
Hylaeus confusus	1	4	0	0	5
Hylaeus gibbus	0	3	0	0	3
Hylaeus hyalinatus	1	1	0	0	2
Lasioglossum albipes	0	2	0	0	2
Lasioglossum calceatum	2	0	0	0	2
Lasioglossum fratellum	0	2	11	9	22
Lasioglossum leucopus	1	0	0	1	2
Lasioglossum rufitarse	0	0	2	2	4
Megachile lapponica	0	0	1	4	5
Megachile versicolor	0	1	0	0	1
Megachile willughbiella	0	0	1	0	1
Nomada glabella	0	0	0	2	2

Nomada leucophthalma	0	0	0	1	1
Nomada rufipes	0	1	0	0	1
Osmia bicornis	1	0	0	0	1
Osmia laticeps	1	0	0	1	2
Osmia nigriventris	0	0	2	1	3
Osmia parietina	1	1	0	0	2
Osmia uncinata	2	0	0	3	5
Sphecodes crassus	0	1	0	0	1
Sphecodes geoffrellus	0	1	0	3	4
Stelis ornatula	1	0	0	0	1
Grand Total	50	86	704	626	1466

Appendix 3. Distribution of number of species between regions and between management regimes within regions.

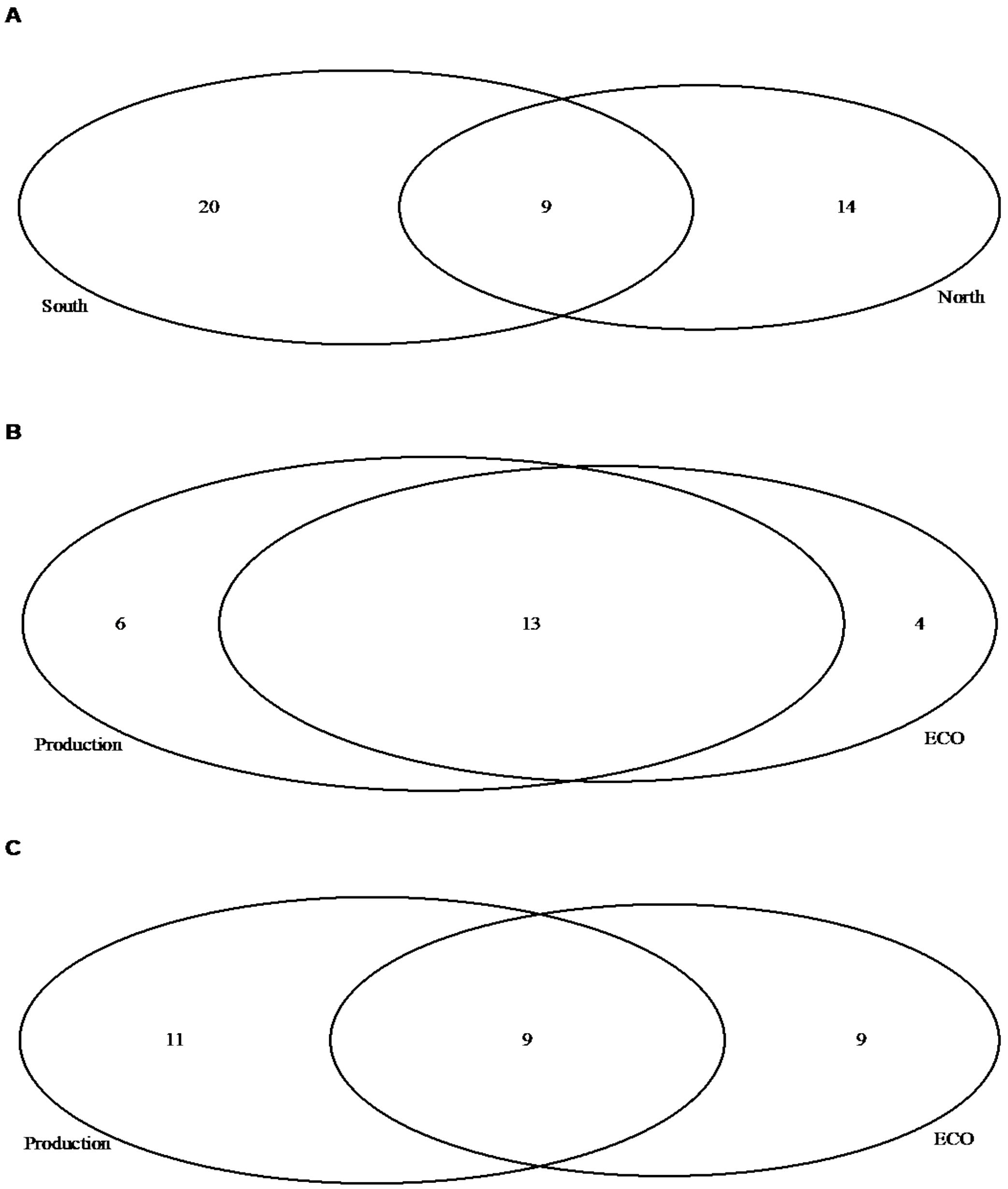

Figure 10. Distribution of number of species between A) regions, B) management regimes within the northern region and C) management regimes within the southern region.

Appendix 4. Stand structure data of each region

Table 6. Stand structure data of each region.

	Northern Sweden	Southern Sweden	p-value
Plots	50	38	
Basal area (m2/ha)	11.5±0.9	11.2±0.9	0.761
Living tree diversity	8.6±0.4	10.1±0.6	0.094
Deadwood volume (m3/ha)	9.4±1.6	6.4±0.8	0.231
Deadwood diversity	10.2±0.9	8.2±0.7	0.126
Open area % - 500m	6.2±0.8	3.5±0.5	0.117
Open area % - 100m	19.9±4.0	9.1±2.1	0.321

Appendix 5. Results of models

Table 7. Results of the best performing models of the whole dataset. Ltdiv = living tree diversity; m3ha = volume of deadwood; dwdiv = deadwood diversity. Highlighted p-values hold statistical significance ($p < 0.05$).

Model: **Abundance**

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
ltdiv	0.943	0.030	0.065	0.0	0.379

Model: **Species richness**

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
abundance	1.018	0.003	**<0.001**	NA	NA
AIC	NA				

Model: **Shannon diversity index**

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
m3ha	0.005	0.005	0.359	0.0	0.426

Model: **Functional dispersion**

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
dwdiv	0.005	0.002	**0.004**	NA	NA
AIC	-156.411				

Model: **Raos' Q**

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
dwdiv	0.002	0.001	**0.003**	0.0	0.898

Table 8. Results of the best performing models of the northern region. m2ha = basal area of living trees; m3ha = volume of deadwood; dwdiv = deadwood diversity; openarea100.0_15 = open area in 100 m radius; ltdiv = living tree diversity. Highlighted p-values hold statistical significance (p <0.05).

Model: Abundance

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
m2ha	0.989	0.013	0.407	0.0	0.506
m3ha	1.010	0.010	0.319		
dwdiv	0.981	0.018	0.318		
openarea100.0_15	0.996	0.003	0.151		

Model: Species richness

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
abundance	1.009	0.003	**0.009**	NA	NA
ltdiv	1.030	0.018	0.092		

Model: Shannon diversity index

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
dwdiv	-0.015	0.010	0.127	0.0	0.984
ltdiv	0.046	0.021	**0.035**		

Model: Functional dispersion

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
dwdiv	0.002	0.001	0.118	0.0	0.40
ltdiv	0.004	0.002	0.080		

Model: Raos' Q

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
dwdiv	0.001	0.000	0.126	0.0	0.37
ltdiv	0.002	0.001	0.101		

Table 9. Results of the best performing models of the southern region. m2ha = basal area of living trees; m3ha = volume of deadwood; dwdiv = deadwood diversity. Highlighted p-values hold statistical significance (p <0.05).

Model: Abundance

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
m2ha	0.973	0.022	0.235	0.0	0.493

Model: Species richness

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
abundance	1.162	0.038	**<0.001**	0.0	0.72
m3ha	1.016	0.019	0.397		

Model: Shannon diversity index

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
m3ha	0.027	0.019	0.147	0.0	0.428

Model: Functional dispersion

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
m3ha	-0.007	0.004	0.154	0.0	0.243
dwdiv	0.015	0.006	**0.023**		

Model: Raos' Q

Predictors	*Estimates*	*SE*	*p-value*	*dAIC*	*weight*
dwdiv	0.003	0.002	0.058	0.0	0.397

Appendix 6. Species composition

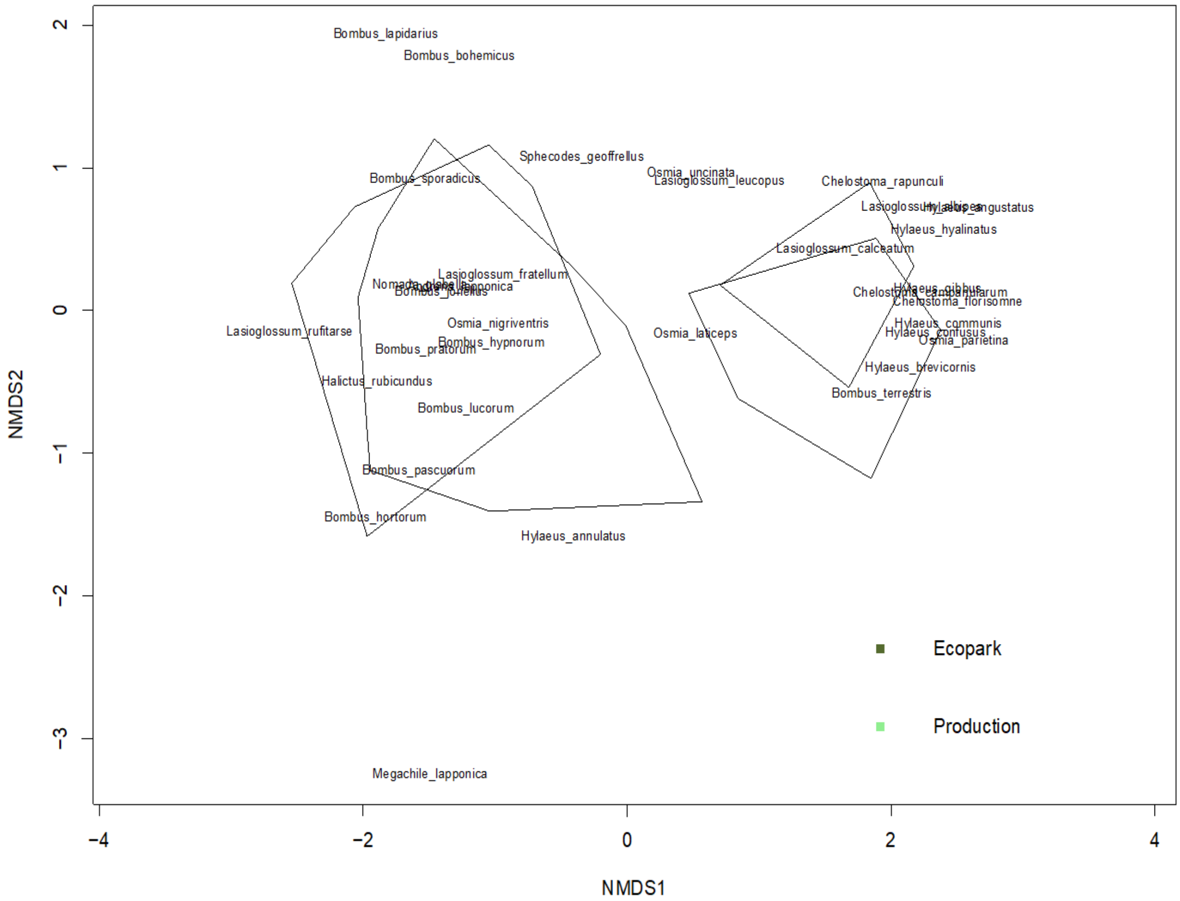

Figure 11. Complete figure of species composition with all the names of the species.

Appendix 7. Map of each study area with positions of plots and target classes

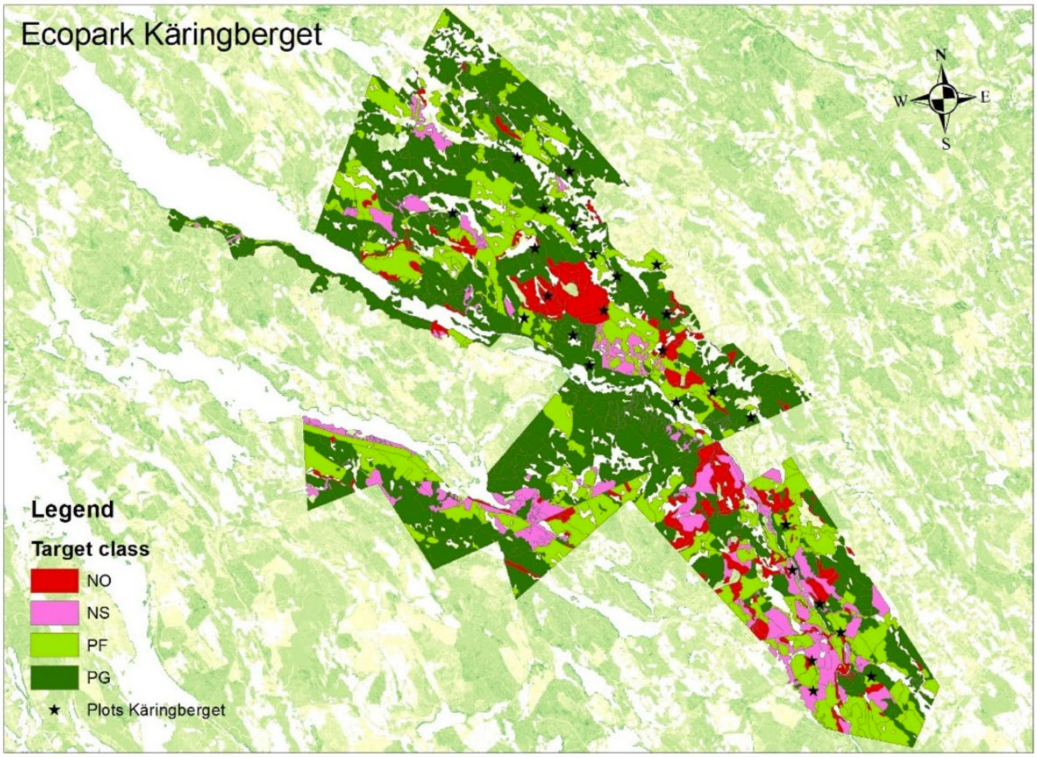

Figure 12. Käringberget ecopark map with positions of sampling plots marked with "" and target classes. NO = Areas with high natural values; NS = Areas dedicated to restoration or management of natural values; PF = Production forests emphasizing natural values; PG = Production forests with no specific natural values.*

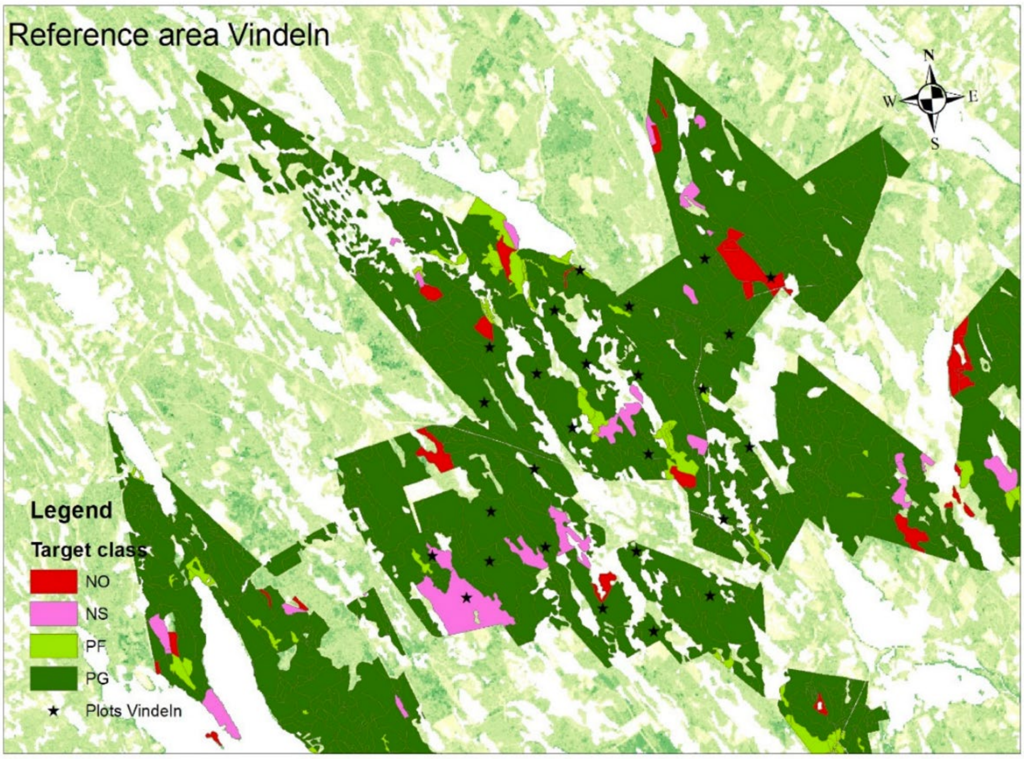

Figure 13. Map of Vindeln production landscape with positions of sampling plots marked with ”” and target classes. NO = Areas with high natural values; NS = Areas dedicated to restoration or management of natural values; PF = Production forests emphasizing natural values; PG = Production forests with no specific natural values.*

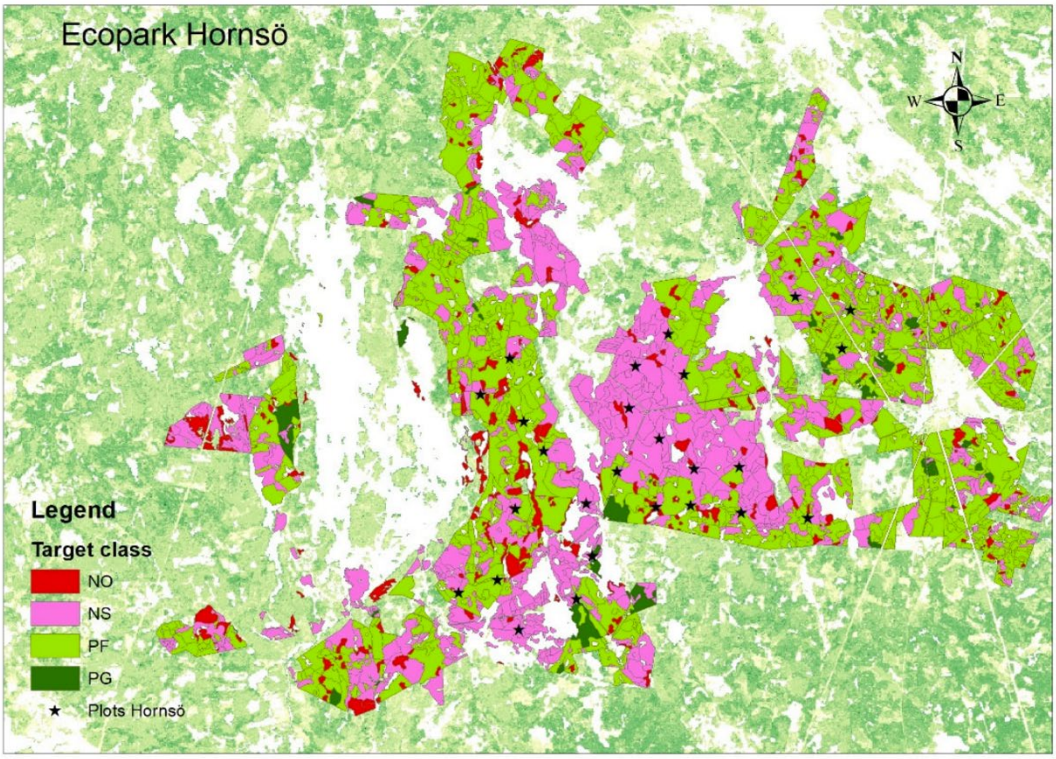

Figure 14. Hornsö ecopark map with positions of sampling plots marked with ”” and target classes. NO = Areas with high natural values; NS = Areas dedicated to restoration or management of natural values; PF = Production forests emphasizing natural values; PG = Production forests with no specific natural values.*

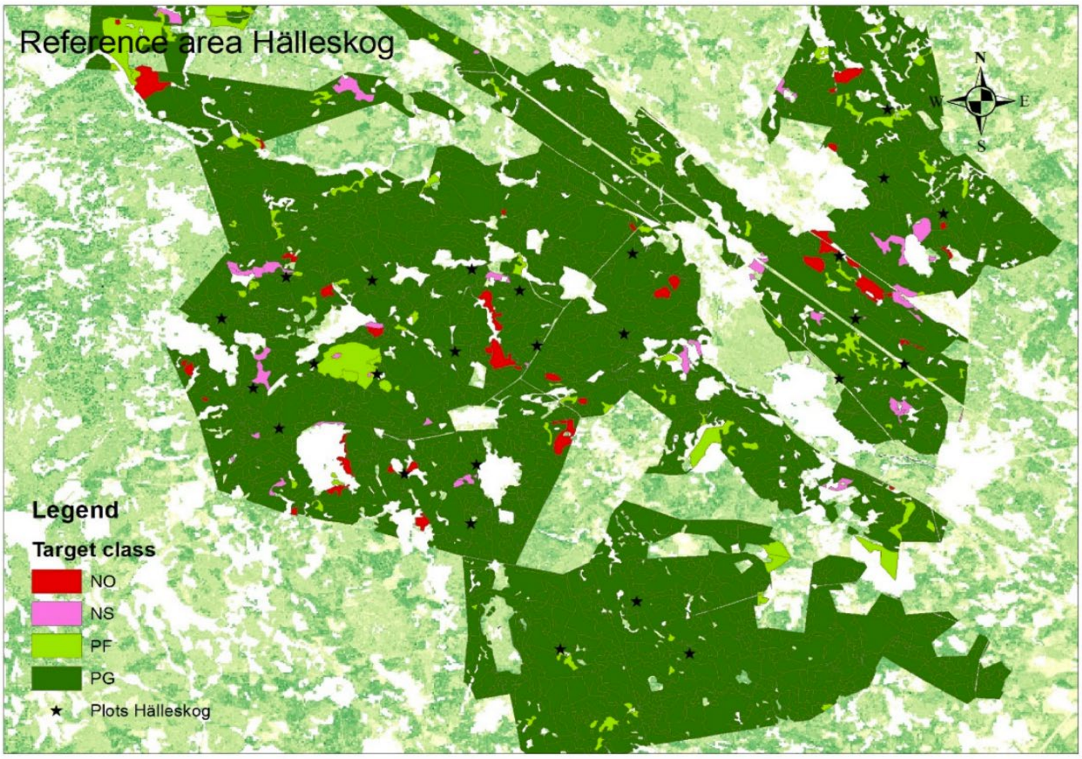

Figure 15. Hornsö ecopark map with positions of sampling plots marked with "" and target classes. NO = Areas with high natural values; NS = Areas dedicated to restoration or management of natural values; PF = Production forests emphasizing natural values; PG = Production forests with no specific natural values.*

Appendix 8. Location of the 500 meters buffer zones in each area and forest age classes

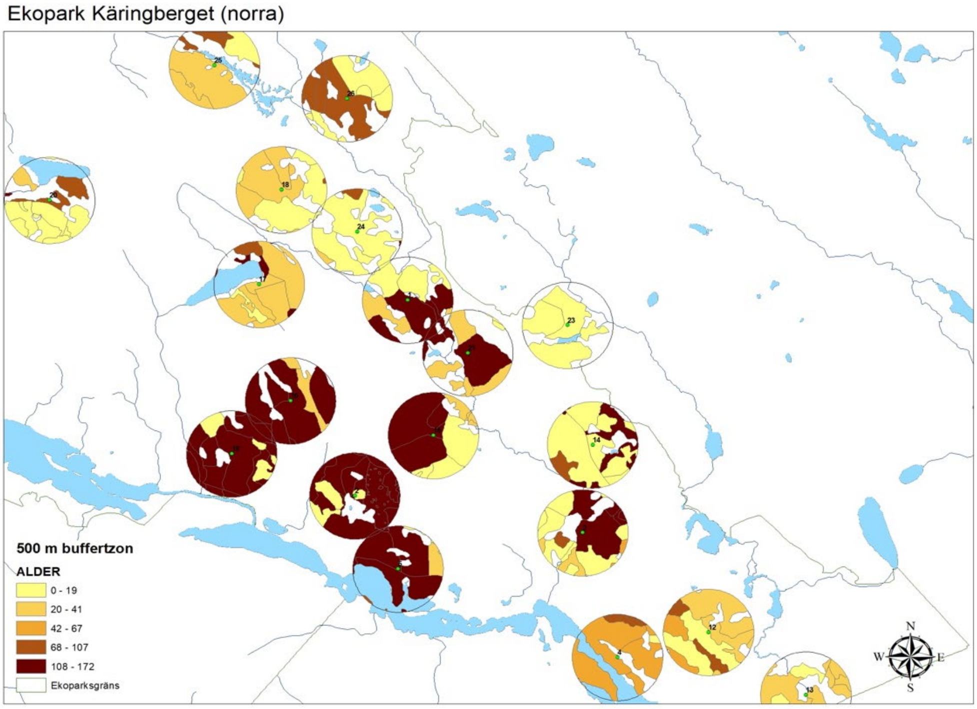
Ekopark Käringberget (norra)

Figure 16. Location of some 500 meters buffer zones in Käringberget ecopark and forest age classes.

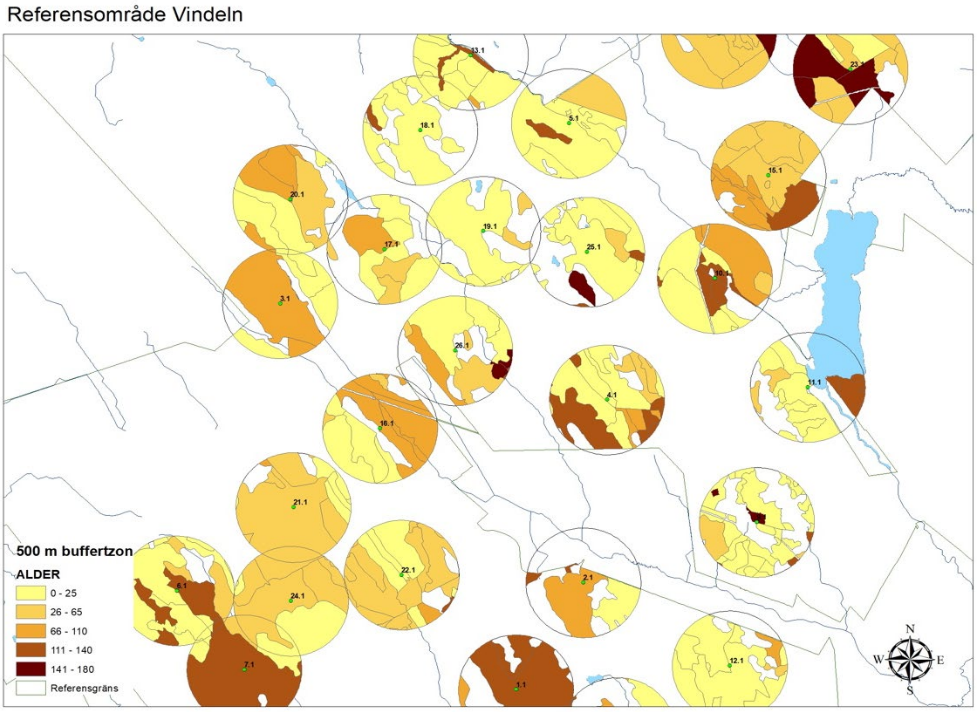
Referensområde Vindeln

Figure 17. Location of some 500 meters buffer zones in Vindeln production landscape and forest age classes.

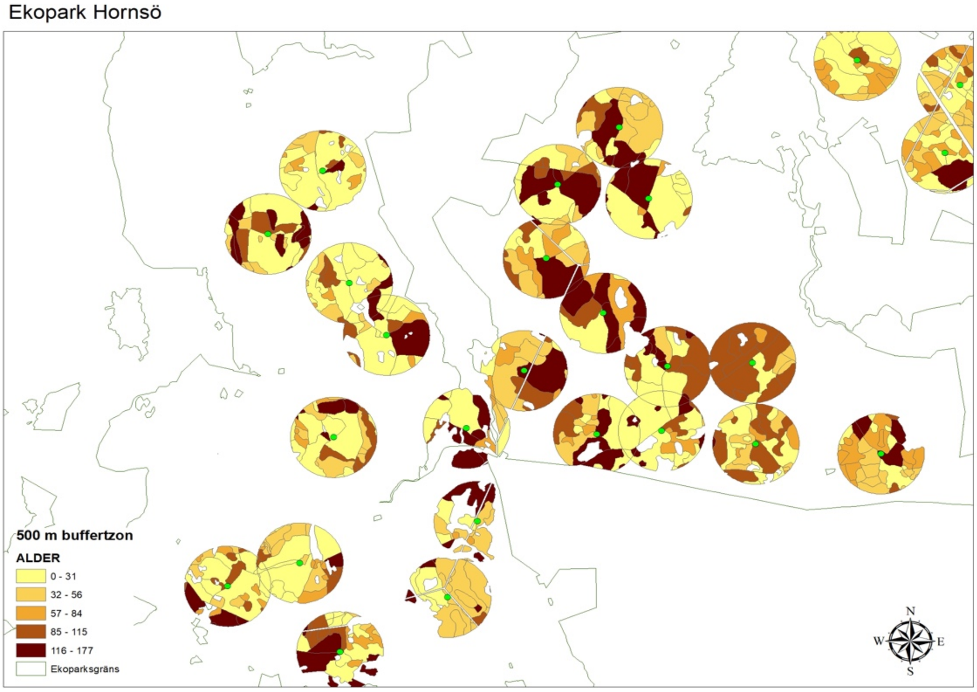

Figure 18. Location of some 500 meters buffer zones in Hornsö ecopark and forest age classes.

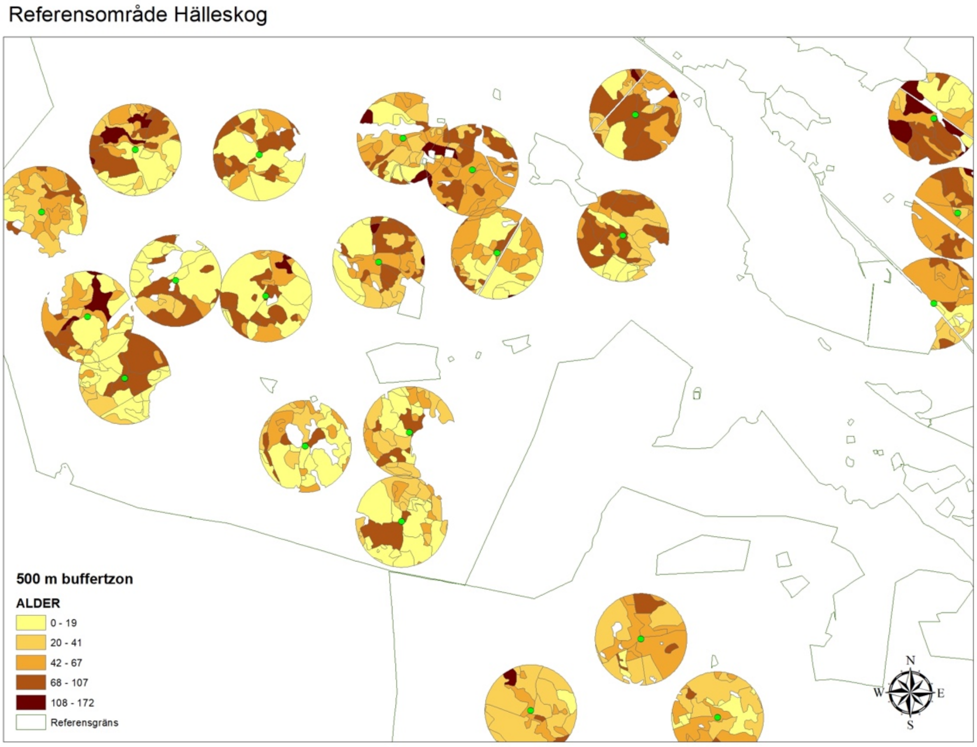

Figure 19. Location of some 500 meters buffer zones in Hälleskog production landscape and forest age classes.

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