Wood-living beetle diversity and Swedish forest management

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2022

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ISBN: 978-91-8009-921-9 (PRINT)
ISBN: 978-91-8009-922-6 (PDF)
Electronic version: http://hdl.handle.net/2077/71971

SVANENMÄRKET
Trycksak
3041 0234

Abstract

Humans have impacted Fennoscandian forests for thousands of years, through grazing, burning, and since the industrial revolution increasingly through efficient industrial forestry. These impacts have changed the composition and structure of these forests, by reducing forest age, simplifying forest structure, and reducing the amount of broadleaved trees, among other things. To achieve a forestry model that is sustainable, the consequences of these changes on forest biodiversity need to be evaluated.

In this thesis, I focus on saproxylic (wood-living) beetles, within south-central Swedish forestry and forest conservation. This ecological group utilizes dead wood in various forms and is species-rich (1,200 Swedish species), threatened (400 red-listed Swedish species), ecologically diverse, and of high conservation and management relevance.

In **Paper I**, I test the 10-year effect of conservation-oriented thinning on oak-associated saproxylic beetles in 8 pairs of 1-hectare oak-dominated forest plots spread across southern Sweden. For each pair, one plot was treated with thinning in 2002/2003, and one was left as a minimal intervention reference plot. Beetles were sampled shortly before, shortly after, and in my study, 10 years after thinning. The number of beetle species in the thinning plots relative to the reference plots increased slightly and non-significantly shortly after thinning, but significantly 10 years later, equaling around a 33% increase.

In **Paper II**, I compare the diversity of saproxylic beetles and several ecological subgroups between a common spruce forestry stage (young pre-commercially thinned stands), and small broadleaf-dominated unmanaged semi-natural stands (Woodland Key Habitats). Ten pairs of stands of the two forest types were used, spread across Jönköping county in southern Sweden. While the local (alpha) diversity of beetles was similar between the forest types, the total (gamma) diversity was higher for red-listed and broadleaf-associated species in the Woodland Key Habitats. Further, the species composition differed between the forest types, and Woodland Key Habitats had higher compositional (beta) diversity.

Paper III uses related but broader comparisons, between middle-aged commercially thinned spruce stands, middle-aged not recently thinned spruce stands, spruce-dominated Woodland Key Habitats and spruce-dominated nature reserves. Here, sampling was spread over two regions, one with higher occurrence of Woodland Key Habitats (Örebro county) and one with lower (Jönköping county). A total of 10 pairs, 10 triplets, and 3 single stands were used. Local diversity was higher in the thinned stands than in Woodland Key Habitats, but did not differ for the other forest types. Total diversity of most ecological groups did not differ between forest types, but red-listed species were more diverse in Woodland Key Habitats than in thinned stands in the region with more Woodland Key Habitats, but not in the region with less. The species composition did not differ between the forest types, but Woodland Key Habitats had higher compositional diversity.

Paper IV combines data from the two previous papers, this time looking at the influence of characteristics of the surrounding landscape on local diversity of saproxylic beetles. Four landscape variables (volume of broadleaf forest, amount of old forest, amount of conservation forest, amount of clear-cut) were examined, at three scales (within 250 m, 1,250 m, and 2,500 m from stands). At the scale of 2,500 m, the volume of broadleaf forest influenced saproxylic beetle diversity positively, while the amount of old forest surprisingly influenced red-listed species negatively.

Overall, the studies show the varied and complex ways management can affect beetle diversity and communities. Beetle diversity patterns are clearly scale-dependent, and aspects of the surrounding landscape are important for local diversity. Thinning seems to have a positive influence on the local number of saproxylic beetle species, in oak and to a certain extent spruce forests, and for the former at least for 10 years. Several common spruce forestry stages have as many or more saproxylic beetle species per stand as nearby conservation stands. However, the managed stages are more homogenous, lowering their contribution to overall saproxylic diversity. Conservation stands, including Woodland Key Habitats, strengthen conservation of Swedish saproxylic beetles. A crucial aspect seems to be the amount and diversity of broadleaved trees, an increase of which both within forestry and conservation should benefit saproxylic beetles.

Keywords: biodiversity, forestry, harvest, insects, landscape, management

Sammanfattning

Mänsklig påverkan på Fennoskandiska skogar har pågått i tusentals år, genom bete, bränning, och sen den industriella revolutionen i ökande grad genom effektiv industriellt skogsbruk. Denna påverkan har förändrat skogarnas sammansättning och struktur, genom minskad skogsålder, förenklad skogsstruktur, minskad mängd lövträd, med mera. För att uppnå ett hållbart skogsbruk krävs att dessa förändringars påverkan på skoglig biodiversitet utvärderas.

I denna avhandling fokuserar jag på vedlevande skalbaggar, inom syd- och mellansvenskt skogsbruk och naturvård. Denna ekologiska grupp utnyttjar död ved i alla dess former, och är artrik (1200 svenska arter), hotad (400 rödlistade svenska arter), ekologiskt variabel, och av stor relevans för vård och skötsel av skogar.

I den första studien testar jag 10-årseffekten av naturvårdsgallring på eklevande vedskalbaggar i åtta par av en hektar stora ekdominerade skogsytor spridda över södra Sverige. I varje par blev en skogsyta naturvårdsgallrad 2002/2003, och en lämnad till fri utveckling som referensyta. Skalbaggar samlades in kort före, kort efter, och i min studie, 10 år efter gallringen. Antalet skalbaggsarter i gallringsytorna relativt till referensytorna ökade något och icke-signifikant kort efter gallringen, men signifikant 10 år senare, motsvarande en ökning på runt 33%.

I den andra studien jämför jag mångfalden av vedlevande skalbaggar och ett antal ekologiska undergrupper mellan ett vanligt skogsbruksstadie (unga röjda granskogar), och små, lövdominerade, obrukade seminaturliga skogar (nyckelbiotoper). Tio par skogar av de två typerna användes, spridda i Jönköpings län i södra Sverige. Den lokala (alfa-) diversiteten av skalbaggar skiljde sig inte mellan skogstyperna, men den totala (gamma-) diversiteten var högre i nyckelbiotoperna för rödlistade arter och arter på lövträd. Dessutom skiljde sig artsammansättningen mellan skogstyperna, och nyckelbiotoperna hade högre kompositionell (beta-) diversitet.

Den tredje studien använder liknande men breddade jämförelser, mellan medelålders gallrade granproduktionsskogar, medelålders ogallrade granproduktionsskogar, grandominerade nyckelbiotoper och grandominerade naturreservat. Här var insamlingarna spridda över två regioner, en med högre förekomst av nyckelbiotoper (Örebro län) och en med lägre (Jönköpings län). Totalt 10 par, 10 tripletter och 3 oparade skogar användes. Lokal diversitet var högre i gallrade produktionsskogar än i nyckelbiotoper, men skiljde sig inte för de övriga skogstyperna. Total diversitet hos merparten av de ekologiska grupperna skiljde sig inte mellan skogstyperna, men rödlistade arter var fler i nyckelbiotoperna än i gallrade produktionsskogar i regionen med fler nyckelbiotoper, men inte i regionen med färre. Artsammansättningen skiljde sig inte mellan skogstyperna, men den kompositionella diversiteten var högre i nyckelbiotoperna.

Den fjärde studien kombinerar data från de två tidigare studierna, denna gång för att undersöka sambandet mellan egenskaper hos det omkringliggande landskapet och den lokala diversiteten av vedlevande skalbaggar. Fyra landskapsvariabler (volym av

lövskog, mängd gammal skog, mängd naturvårdsskog, mängd hygge) undersöktes, i tre skalor (inom 250 m, 1250 m och 2500 m). Inom 2500 m påverkade volymen lövskog vedlevande skalbaggar positivt, men mängden gammal skog påverkade överraskande nog rödlistade arter negativt.

Sammantaget visar studierna de varierade och komplexa sätt som skogsskötsel kan påverka diversiteten och sammansättningen av vedlevande skalbaggssamhällen. Diversitetsmönster hos skalbaggar är tydligt beroende av skalan som mätningar sker på, och aspekter hos det omkringliggande landskapet är viktiga för lokal diversitet. Gallring verkar ha en positiv inverkan på det lokala antalet skalbaggsarter, i ek- och till viss del granskogar, och för de förra i minst 10 år. Flera vanliga stadier av granproduktionsskogar har lika många eller fler arter av vedlevande skalbaggar per skogsparti som närliggande naturvårdsskogar. Produktionsskogar är dock mer homogena, vilket minskar deras bidrag till den övergripande vedlevande diversiteten. Naturvårdsskogar, inklusive nyckelbiotoper, förstärker bevarandet av svensk vedlevande skalbaggsdiversitet. En avgörande aspekt verkar vara mängden och diversiteten av lövträd, och en ökning av dessa inom både skogsbruk och naturvårdsskötsel bör gynna vedlevande skalbaggar.

List of papers

Paper I

Gran O, Götmark F. 2019. Long-term experimental management in Swedish mixed oak-rich forests has a positive effect on saproxylic beetles after 10 years. *Biodiversity and Conservation*, 28:1451–72.

Paper II

Gran O, Götmark F. 2021. Saproxylic beetles in pre-commercially thinned Norway spruce stands and woodland key habitats: How do conservation values differ? *Forest Ecology and Management*, 479:118584.

Paper III

Gran O. 2022. Lower alpha, higher beta, and similar gamma diversity of saproxylic beetles in unmanaged compared to managed Norway spruce stands. *PLOS One*, 17:e0271092.

Paper IV

Gran O. 2022. Wood-living beetle diversity is enriched by broadleaf forest, but not old forest, in a conifer forestry landscape. *Manuscript*.

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1 Background

1.1 Saproxylic beetle diversity

A majority of Earth's described species are insects, and more than a third of all described insects are beetles (Chapman 2009, Stork 2018). With nearly 400,000 described species globally, this single order (Coleoptera) of insects contains more species than all plants and chordates combined (Fig. 1). Most beetle diversity still remains to be described, with recent estimates for the total number of beetle species on Earth around 1.5 million (Stork et al. 2015). Consequently, beetles should have a central role in efforts to conserve the planet's rich biodiversity. Despite this, and despite recent hotly debated and widely publicized reports on global insect declines (Cardoso et al. 2020, Van Klink et al. 2020, Daskalova et al. 2021, Wagner et al. 2021), this megadiverse group is still underprioritized in conservation (Cardoso et al. 2011, Godet and Devictor 2018, Samways et al. 2020).

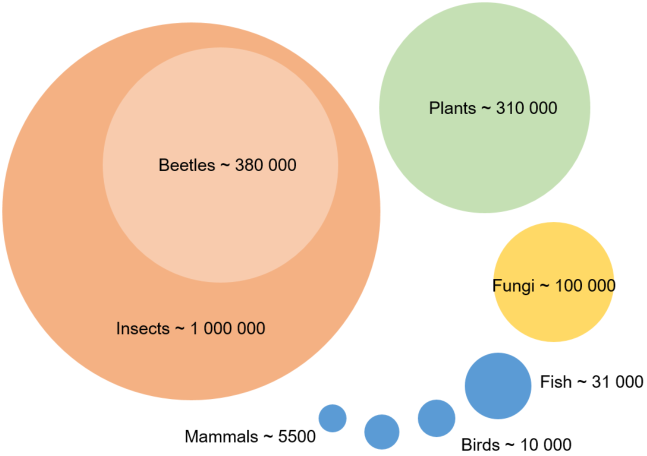

Figure 1. Estimated number of described species globally. Based on Chapman (2009).

The diversity of beetles is not only a matter of the number of species. Beetles occupy virtually every terrestrial and freshwater habitat, and are tremendously varied in morphology and ecology (Gullan and Cranston 2014). This thesis concerns one ecological subset of beetles, the *saproxylic beetles*. A saproxylic, or wood-living, species is one which "depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened or dead trees" (Speight 1989, Stokland et al. 2012). The focus of this thesis is on the most well-studied saproxylic beetle fauna, that of central-northern Europe, and more specifically that of the hemiboreal zone of Sweden. Unless otherwise noted, what is outlined below should be viewed within this geographic context.

Saproxylic species are found in many animal and fungal groups, but are especially numerous among the beetles. In the Nordic countries, there are about 1,500 saproxylic beetle species (Stokland et al. 2012). In Sweden, there are around 1,200 (SLU SSIC 2022). This represents about a quarter of all forest-living species (Siitonen 2001) and forest-living insect species (Ulyshen and Šobotník 2018), and between a quarter and half of all beetle species (Graf et al. 2022) in central-northern Europe.

Besides being one of the most diverse species groups, saproxylic beetles are also among the most threatened. On the European red-list of saproxylic beetles, around 20% of evaluated species are classified as threatened, and more than half are red-listed (Cálix et al. 2018). Beetles are the most numerous group on the Swedish red-list, with 400 saproxylic beetle species red-listed (SLU SSIC 2020). The main causes of decline are judged to be intensified forestry, loss of veteran trees, decline in coarse dead wood (especially of broadleaves), denser forests, and a lack of both old-growth forest and natural early successions (Larsson et al. 2011, Eide et al. 2020). Beside intrinsic value as a substantial part of forest biodiversity, saproxylic beetles are also important for forest ecosystem functioning and resilience (Stokland et al. 2012).

Saproxyly is not contained to a single branch of beetle phylogeny, instead having representatives in most of the terrestrial beetle families. As the broad definition of *saproxylic* above hints at, there are many ways of being wood-living. Although a more detailed taxonomy of the feeding ecology of saproxylic beetles can be made (e.g. Bouget et al. [2005], Möller [2009]), roughly speaking they fall into four major feeding guilds (as outlined in Stokland et al. [2012]):

- *Wood consumers*, also called detritivores or saprophages. These feed directly upon the woody material itself. Many are early colonizers of fresh dead wood, feeding on the nutrient- and energy-rich phloem or cambium under the bark during the first year or two. Others feed on the heart- or sapwood itself, mostly during later successional stages (Esseen et al. 1992).
- *Fungivores*. These feed on saproxylic fungi, either in the form of fruiting bodies or mycelia.
- *Predators*. These feed on other living saproxylic animals, often other beetles.
- *Scavengers*, also called necrophages. These feed on the dead organic remains of other saproxylic animals.

Note that the feeding biology of saproxylic beetles often refers primarily to that of the larva, as the adult stage of many species is short-lived. The divisions between these feeding guilds are not straightforward, and many species fall into more than one category. Especially hazy is the distinction between wood consumers and fungivores, as there is a tight association between saproxylic fungi and beetles (Birkemoe et al. 2018). Beetles cannot digest cellulose without the help of fungal or microbial mutualists, and many species feed on dead wood infused with mycelia, in the process of decomposition. Furthermore, knowledge of the specific feeding biology of saproxylic beetles is in many cases lacking, and based on anecdote or old, hard-to-verify claims.

1.2 Substrate and habitat requirements

One probable factor explaining the high diversity of saproxylic beetles is the high diversity of dead wood substrates (Ulyshen and Šobotník 2018). Dead wood can vary in many aspects, each more or less important in determining the diversity and species composition of the inhabiting saproxylic beetles. Combined, these aspects produce an almost endless combination of dead wood types (see e.g. Stokland et al. [2012] Fig. 12.6).

One of the most fundamental characteristics of dead wood is the *species of tree*. Most saproxylic beetles in Sweden can utilize more than one tree species, but there are clearer divisions between tree genera, and especially between broadleaves and conifers (Jonsell et al. 1998, Dahlberg and Stokland 2004, Stokland et al. 2012, Vogel et al. 2020). Figure 2 shows, for each tree genus, the number of associated saproxylic beetle species. More species are found on broadleaves as a group than on conifers, and this is especially true for red-listed species (Berg et al. 1994, Jonsell et al. 1998, Jonsson et al. 2005, Lindbladh et al. 2007). Oaks, *Quercus robur/petraea,* are of especial importance, with nearly 700 associated saproxylic beetle species in Sweden, and the highest number of red-listed species (SLU SSIC 2022).

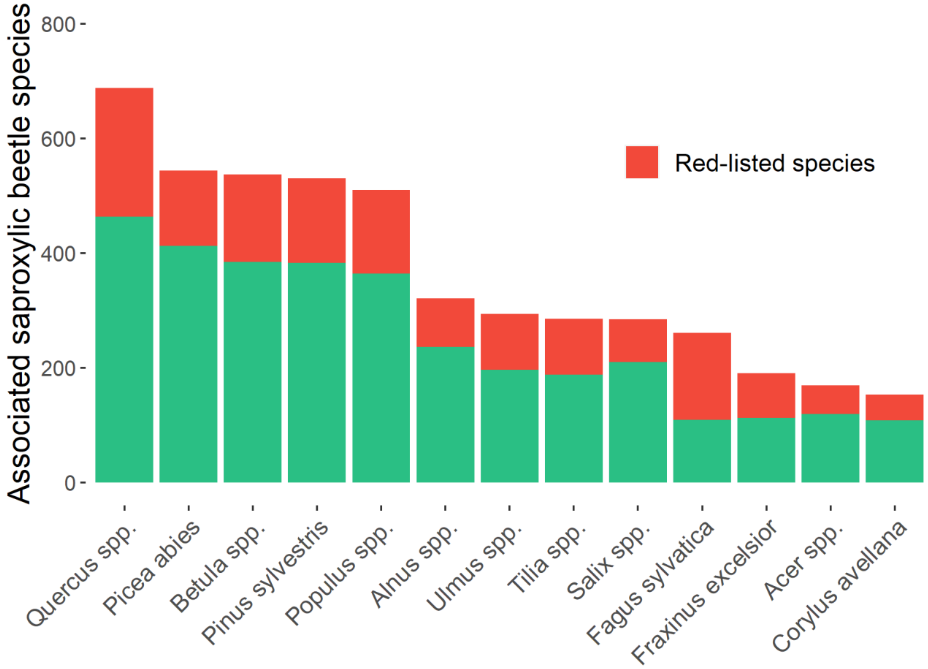

Figure 2. The number of saproxylic beetle species associated with Swedish tree taxa. Based on SLU SSIC (2022).

Microclimate, especially *sun-exposure and temperature*, is another factor seemingly important to the diversity of saproxylic beetles, with generally more species found in sun-exposed conditions (Gärdenfors and Baranowski 1992, Jonsell et al. 1998, Gossner et al. 2013, Lachat et al. 2016, Seibold et al. 2016). Importantly however, the degree of openness influences the composition of saproxylic beetle communities, such that there is a largely separate fauna associated with sun-exposed, open habitats compared to closed-canopy, shady habitats (Müller et al. 2010, 2020, Bouget et al. 2014, Johansson et al. 2017, Vogel et al. 2020). Although fewer than the sun-loving species, still around a third of saproxylic and red-listed saproxylic beetle species prefer shade (Jonsell et al. 1998, Lindhe et al. 2005). Other microclimatic factors such as humidity are much less studied, but may be important as well (Johansson et al. 2017). A potentially important caveat for many of the studies showing a higher number of saproxylic beetle species in sun-exposed habitats is that flight activity increases with temperature. The effect could partly or primarily be caused by a higher number of individuals caught by flight-interception traps in warm conditions (Müller et al. 2010, Bouget et al. 2013). Controlling for the number of individuals, e.g. through the use of species accumulation curves with individuals on the x-axis, should get around this but is not always used in this literature.

As dead wood decays (mostly as a result of fungal activity), the compositional and structural properties of the wood changes. Following these changes, there is a clear succession of saproxylic beetle species over the lifespan of the dead wood object (Esseen et al. 1992, Stokland et al. 2012). As such, *decay stage* is important in determining the saproxylic beetle community (Müller et al. 2020). Among red-listed saproxylic beetles, there are many species associated with each stage of decay, although many utilize the middle of the spectrum (2-15 years) (Jonsell et al. 1998).

There are other characteristics of dead wood, each of which may be important in determining saproxylic beetle species composition. These include the *part of the tree* (root, stem, branch), the *specific tissue* (bark, inner bark or wood), other types of substrate like tree cavity (Berg et al. 1994, Jonsell et al. 1998, Bouget et al. 2014) or beetle larval galleries, the *position* of the wood (Ranius et al. 2015, Gandiaga et al. 2018), and the *size* of the dead wood object. For the latter, many species prefer coarser dead wood (Jonsell et al. 1998, Seibold et al. 2015) although the diversity associated with fine dead wood may be overlooked (Schiegg 2003, Lindhe et al. 2005, Jonsell et al. 2007, Jonsell 2008).

Finally, interactions with wood-decaying *fungi* are very important for many saproxylic beetles (Birkemoe et al. 2018). At a broad level, the distinction between brown and white rot seems important in determining the saproxylic beetle community, although associations with specific fungi species or genera are also common (Stokland et al. 2012).

Further increasing the complexity of saproxylic beetle substrate requirements is the fact that many of these factors interact. This is especially true for tree species, which mediates and is mediated by the influence of several other factors. For example, the importance of tree species in determining the saproxylic beetle community decreases as the wood decays and the beetle species composition is determined more by what fungal taxa have colonized (Jonsell et al. 1998, Wende et al. 2017). The influence of sun-exposure is also dependent on tree species, with saproxylic beetles generally having similar preferences as their host tree (Gärdenfors and Baranowski 1992). As such, a preference for sun-exposed dead wood is more common in species on pioneer broadleaves such as aspen, *Populus tremulae*, and birch, *Betula pendula/pubescens*, than on late-successional Norway spruce, *Picea abies* (Jonsson et al. 2005, Johansson et al. 2017). The two tree taxa most in focus in this thesis, oaks and spruce, largely represent the two opposite ends of the spectrum. For many spruce-associated species, closed canopy and microclimatic continuity are preferred (Koivula and Vanha-Majamaa 2020), while most oak-associated species prefer sun-exposed habitat and may be threatened by abandonment of traditional wood pastures and closing tree canopies (Gärdenfors and Baranowski 1992, Franc and Götmark 2008, Vodka et al. 2009, Siitonen and Ranius 2015, Miklín et al. 2018). This picture is simplified, as shown by Müller et al. (2010) who found an increasing number of spruce-associated beetles in open habitat, probably as a result of the rich fauna associated with clusters of trees killed by the European spruce bark beetle, *Ips typographus*.

The influence of the *amount of dead wood* in a forest on the diversity of saproxylic beetles is a much studied subject. The general idea is that the species-area relationship (Arrhenius 1921), in which the number of species in an ecosystem increases with the amount of available habitat, should be extendable to saproxylic beetles and the amount of dead wood (Martikainen et al. 2000, Stokland et al. 2012). There are many studies both confirming (Seibold and Thorn 2018, Jokela et al. 2019) and failing to confirm (Brin et al. 2009, Lassauce et al. 2011, Bouget et al. 2013, Ranius et al. 2015) this relationship. Some of the studies finding a relationship have converged on thresholds of the amount of dead wood below which the diversity of saproxylic beetles decreases quite rapidly, although such thresholds have been criticized as simplistic (Ranius and Fahrig 2006, Müller et al. 2010). For boreal coniferous forest, such a threshold seems to be somewhere around 20 m^3/ha, and possibly higher for temperate broadleaf forest (Martikainen et al. 2000, de Jong and Almstedt Jansson 2005, Müller and Bütler 2010). The average amount of dead wood in Swedish forests is around 8.5 m^3/ha (Nilsson et al. 2019).

In many situations, the *diversity of dead wood* may be more important for saproxylic beetle diversity than the total volume (Lassauce et al. 2011, Bouget et al. 2013, Ranius et al. 2015, Seibold et al. 2016), though there are exceptions (Larsson Ekström et al. 2021) and the two are usually correlated (Seibold and Thorn 2018). For red-listed species specifically, the diversity of dead wood may be less important than for saproxylic beetles in general, as many of them are associated with a similar set of rare substrates such as large diameter wood and veteran trees (Hottola et al. 2009).

1.3 Dispersal and continuity

Most of the ecological theories proposed to explain the differential occurrence and diversity of species in nature (community assembly) lean more or less heavily on one or both of two processes: niche selection and dispersal (Vellend [2016], Leibold and Chase [2017]; there are other processes, such as ecological drift and speciation, that may be important as well). The theories emphasizing niche selection, also known as species sorting or environmental filtering, propose that species occur where they are adapted to the local environment, i.e. where they have an adaptive advantage. For saproxylic beetles, environmental variables of interest would then be those outlined in the previous section – species associated with veteran broadleaf trees will occur where those trees occur, etc. In the other view, emphasizing dispersal limitation, species are not perfectly distributed across the landscape in the habitats that suit them. Instead, habitat patches may not be “fully stocked” with the species that could in theory occupy them, as these first have to find their way there. Here, the variables of interest are on one hand the spatial (and temporal) configuration of habitats in the landscape (the degree of fragmentation, distance between patches, longevity of patches), and on the other hand the dispersal ability of each species.

A subset of theories emphasizing dispersal which would seem to well describe the dynamics of saproxylic beetles are the patch dynamic or metapopulation models (Hanski 1999). In these, suitable habitat patches occur interspersed in an inhospitable matrix, and the "population of populations" of a species (metapopulation) persists as long as local population extinctions are compensated by colonizations. This could describe saproxylic beetles at the substrate scale, as ephemeral dead wood substrates are created, colonized, and decay (Jonsson et al. 2005, Stokland et al. 2012). This introduces a temporal aspect to the habitat patches lacking in classical metapopulation models (Ranius et al. 2014), but otherwise matches quite well. The ephemeral nature of dead wood means that to some extent, all saproxylic beetles are adapted to dispersal (Jonsson et al. 2005). At the habitat scale, forests are dynamic, going through successional changes and disturbance events, creating a shifting mosaic (Perry et al. 2008). Although this shifting mosaic dos not perfectly match the simplified metapopulation models of habitat patches and inhospitable matrix, rather consisting of a variegated landscape with gradients of habitat suitability (Brockerhoff et al. 2008, Perry et al. 2008), it is nonetheless clear that dispersal is a key factor influencing the distribution and diversity of saproxylic beetles (Ranius 2006).

Knowledge of the dispersal ability of individual saproxylic beetle species is poor, with only a handful of species having been studied. Estimated dispersal abilities vary greatly, but for most species may be relatively good (Ranius 2006, Brin et al. 2016, Feldhaar and Schauer 2018). At the same time, several studies show an influence of the composition of the surrounding landscape on the local diversity of saproxylic beetles, (Økland et al. 1996, Gibb et al. 2006, Bouget and Parmain 2016, Rubene et al. 2017) indicating that considering scales larger than the local may be important (Jonsson et al. 2005, Bouget and Parmain 2016), especially for red-listed species (Kotiaho et al. 2005, Götmark et al. 2011, Lachat and Müller 2018). However, effects of the spatial configuration of habitat patches (i.e. degree of fragmentation) are hard to disentangle from effects of habitat amount (Fahrig 2003), and some have argued that the latter is more important (Komonen and Müller 2018, Watling et al. 2020).

Both local environmental variables and dispersal ability interact with the concept of continuity, i.e. the degree of persistence of a habitat, which seems important for several species (Nordén et al. 2014). A species adapted to substrates or habitats that are especially ephemeral will need to be good at dispersal, while those adapted to long-lived substrates or habitats do not need to disperse as often or as well (Jonsson et al. 2005, Stokland et al. 2012, Brin et al. 2016, Feldhaar and Schauer 2018). Early-successional forest stages are often ephemeral in nature, with a short-lived post-disturbance phase and quickly-decaying fine wood, although grazing or other continued disturbance may make this stage persist longer. Late-successional stages are more persistent, with slowly decaying coarse wood and veteran trees of long-lived species such as spruce or oak. Viewed the opposite way, the degree to which habitat continuity is important for a species depends on its degree of dispersal limitation (Nilsson et al. 2001, Jonsson et al. 2005, Stokland et al. 2012, Brin et al. 2016, Jonsell et al. 2019). At the same time, continuity interacts with local environmental variables, as certain habitats and substrates such as old-growth forest take a long time to form (Nilsson and Baranowski 1993, Esseen et al. 1997, Lachat and Müller 2018). Consequently, it can be hard to determine if species are dependent on continuity per se (due to dispersal limitation) or on the substrates and structures created by continuity (Kouki et al. 2001, Nordén and Appelqvist 2001, Seibold and Thorn 2018). It may be that both aspects are important (Janssen et al. 2017).

1.4 Fennoscandian forest history

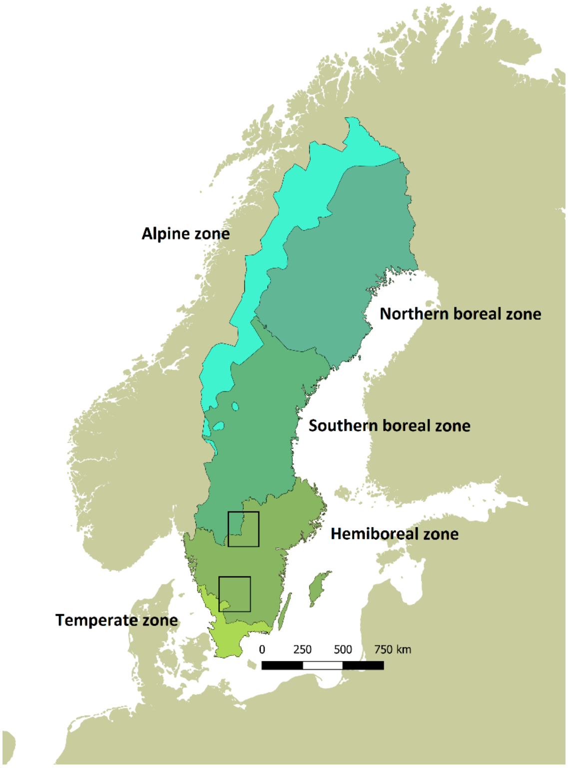

Figure 3. Approximate biogeographic zones of Sweden. The studies in this thesis were all done in the hemiboreal zone, within the two marked rectangular regions (roughly Örebro county in the north and Jönköping county in the south).

This thesis concerns south-central Sweden, a biogeographic transition zone between the temperate forests of southern Sweden and mainland Europe, and the boreal forests of northern Sweden and the greater Eurasian taiga (Fig. 3). The exact borders and name of this zone varies, with some calling it the hemiboreal zone, the boreonemoral zone, or simply the northern edge of the temperate zone. This means that dynamics of both the temperate forests of the south and the boreal forests of the north are at work. The natural forest dynamics of this zone, from the last ice age ~12,000 years ago up until humans started to transform forests some 5,000 years ago (Esseen et al. 1997), are debated. The traditional view has been that these were governed primarily by frequent (once every 50-100 years), large-scale, stand-replacing fires, resulting in largely even-aged forests containing much regenerating habitat (Berglund and Kuuluvainen 2021). Since the 1990s, this view has been challenged by the view that small-scale gap dynamics were much more important and large-scale disturbances rare (fires every 200-500 years on average, Kuuluvainen [2009]). In this new view, forests were governed by small-, medium- and large-scale dynamics, in descending order of importance (Kuuluvainen 2009, Berglund and Kuuluvainen 2021). This created a complex mosaic with disturbances working at different scales, and likely resulted in the majority (at least 50%) of forests being old-growth and multi-layered (Pennanen 2002, Berglund and Kuuluvainen 2021). In the temperate zone, the degree of openness and the way openness was maintained has also been debated, as many species associated with open habitat were seemingly common even before humans opened up forests. Vera (2000) suggested this could be explained by large wild herbivores. Likely a combination of factors such as herbivores, fire, windthrow, flooding, and topography and soils maintained openness in some areas, while most of the forest had a closed canopy (Svenning 2002).

Following reforestation after the last ice age, forests in the hemiboreal zone of Fennoscandia were dominated by a mix of Scots pine (*Pinus sylvestris*), and broadleaves such as birch, lime (*Tilia* spp.), and others (Björse and Bradshaw 1998, Lindbladh et al. 2000). Some 2,000 years ago, oak was common in the area (Lindbladh and Foster 2010), while Norway spruce was rare (Björse and Bradshaw 1998), having arrived just 2500 years before present (Lindbladh et al. 2014). The impact of humans on these forests, having started at least 5,000 years ago, varied in timing and intensity across Fennoscandia, even in the south (Nilsson et al. 2005). Many northern areas remained untouched for much longer (Kouki et al. 2001). Early human impacts consisted of gradually opening up the forest through grazing and slash-and-burn agriculture (Esseen et al. 1997, Kouki et al. 2001).

While burning likely benefitted early-successional species such as pioneer broadleaves and pine (Lindbladh et al. 2014), grazing in combination with climatic effects led to an increase in spruce and a decrease in broadleaves (Lindbladh et al. 2000, 2014, Nilsson et al. 2005). From roughly 1,000 years ago, human activity overtook climatic factors as the cause of spruce spreading at the expense of broadleaves, even more rapidly than before (Lindbladh et al. 2000). In the northern study region in this thesis (~Örebro county), spruce was at this point the dominant tree species, but not in the southern study region (~Jönköping county, Björse and Bradshaw [1998]). From the middle-ages onward, south-central Sweden saw waves of deforestation and reforestation following agrarian expansion and abandonment (Lagerås 2007). By this point, mainland Europe had already seen large-scale deforestation (Kirby and Watkins 2015). Widespread mining, starting already in the middle-ages, caused a high demand for lumber (Barklund 2009). By the 1400s, fires were frequent (fire frequencies as high as once every 20 years), many of them likely human in origin (Niklasson and Drakenberg 2001, Nilsson et al. 2005).

The next few hundred years saw increasing deforestation in southern Fennoscandia, as human use of forests increased. This led to a further reduction in broadleaves, but also a stop to the expansion of spruce, as forests were replaced with open areas (Lindbladh et al. 2000, 2014, Nilsson et al. 2005). Oaks were a special case, as they became protected property of the state in 1558, for future use as naval timber (Eliasson and Nilsson 2002). They now grew large in grazed, agricultural areas and likely benefitted from the open landscape (Nilsson et al. 2005). By the 1600s, large parts of southern Sweden were deforested (Esseen et al. 1992). Mining intensity increased, as did human and cattle populations. Overexploitation of southern forests meant forestry activity had to move northward (Esseen et al. 1997). Mining activity, with associated forest use, was especially prevalent in Bergslagen, near the northern study region in this thesis (~Örebro county, Esseen et al. [1992]). Extensive multiple uses of forests, including for potash, tar, timber, grazing, and slash-and-burn agriculture, continued up until industrialization, with the peak of deforestation occurring in the mid-1800s (Esseen et al. 1997, Barklund 2009, Lindbladh et al. 2014). At the same time, felling of large oaks had begun in the late 1700s, driven in part by naval demand, and in part by intense hatred of oaks from farmers who saw them as ruining their hay meadows (Eliasson and Nilsson 2002). In 1830, the royal protection of oaks ended, resulting in massive cutting and reduction in oak numbers (Eliasson and Nilsson 2002, Lindbladh and Foster 2010). At the same time, heavy grazing likely prevented regeneration of oak (Nilsson et al. 2005).

The start of industrialization in the mid-1800s saw the advent of sawmills, and an increased demand for lumber (Esseen et al. 1997, Barklund 2009). Cutting was still selective, and occurred primarily along rivers (Esseen et al. 1997, Kuuluvainen et al. 2012). Towards the end of the 1800s, the demand for pulp began, for which spruce was the primary tree (Esseen et al. 1997, Barklund 2009). The overexploited southern forests forced the timber front to stretch further northward (Esseen et al. 1997). There was a move from traditional land management towards modern forms, with the end of slash-and-burn agriculture and forest grazing (Lagerås 2007, Lindbladh et al. 2014). Simultaneously, large-scale fire-suppression began, and the high fire frequencies of the preceding 500 years ended (Niklasson and Drakenberg 2001, Nilsson et al. 2005). These changes resulted in reforestation of large areas of abandoned rural land during the early 1900s, and this reforestation was dominated by spruce (Lagerås 2007, Barklund 2009, Lindbladh et al. 2014). The absolute numbers of several broadleaf species increased, but decreased in proportion relative to spruce (Lagerås 2016). The reforestation by spruce instead of broadleaves was especially pronounced in the southern study region in this thesis (~Jönköping county, Lindbladh et al. [2014]).

In the 1940s, the selective cutting forestry model was considered increasingly unsustainable, and was replaced by even-aged clear-cutting (Esseen et al. 1992, Barklund 2009, Kuuluvainen et al. 2012). Rationalization and increased productivity allowed for continued reforestation at the same time as yields increased (Barklund 2009). In the first half of the 20th century, most spruce regeneration had been natural (Lindbladh et al. 2014), but from the 1950s planting became more common (Esseen et al. 1997). Although early clear-cutting methods benefitted broadleaf pioneer species such as birch (Linder and Östlund 1998), soon these were actively combatted, including with herbicides (Esseen et al. 1997, Linder and Östlund 1998). From the 1970s onward, increased grazing pressure from wild ungulates limited broadleaves (Björse and Bradshaw 1998) causing particular regeneration problems for oaks (Petersson et al. 2019).

The 1970s and early 1980s saw the beginning of biodiversity considerations within Swedish forestry (Bush 2005, Götmark et al. 2009), with a new forestry law (Skogsvårdslagen 1979:429). Early forms of retention forestry began (Bush 2005, Kruys et al. 2013, Koivula and Vanha-Majamaa 2020), followed by further biodiversity considerations, such as Woodland Key Habitats (see section 1.5) and voluntary set-asides interspersed in the forestry landscape (Felton et al. 2020). The main push for increased biodiversity considerations happened during the 1990s with new certifications, guidelines, and a new forestry act (Skogsvårdsförordningen 1993:1096), in theory giving equal weight to conservation and production (Esseen et al. 1997, Felton et al. 2020). The last 30 years have seen less dramatic conservation progress and increasing debate around forestry. However, there have also been increases in the amount of large diameter dead wood, large living trees, and tree species diversity in Swedish forests, albeit not nearing natural levels (Kruys et al. 2013, Felton et al. 2020, Kyaschenko et al. 2022). Together with these positive changes is also an increasing influence from climate change, with resultant droughts, fires, and attacks from tree-killing bark beetles (Hof and Svahlin 2016, Biedermann et al. 2019, Hlásny et al. 2021).

Today, Swedish forest cover is back to its pre-medieval extent (Lagerås 2016), with roughly 2,200,000 ha of forested land (around 80% forest cover, Nilsson et al. [2019]). This makes Sweden the nation with the largest area of forest in Europe (Forest Europe 2020). At the same time, the history outlined above, together with the fact that the large majority of Fennoscandian forests are now utilized for wood production through highly efficient forestry (Esseen et al. 1997), means that these forests are dramatically changed from a more natural state. Clear-cutting has replaced natural disturbance regimes based on fire and small-scale disturbances (Esseen et al. 1997, Axelsson and Östlund 2001, Kuuluvainen 2009), resulting in forests going from multi-aged, structurally complex stands to simplified even-aged stands (Axelsson and Östlund 2001, Kuuluvainen 2009). Forests are now denser and less open (Linder and Östlund 1998, Ericsson and Östlund 2000, Hultberg et al. 2014), and dead wood has decreased both in amount and diversity (Esseen et al. 1997, Siitonen 2001, Kuuluvainen 2009). There has been a major decrease in the amount of old-growth forest and old trees (Esseen et al. 1997, Linder and Östlund 1998, Axelsson and Östlund 2001, Kuuluvainen 2009). As outlined above, the history of broadleaves in Fennoscandia during the last 2,000 years is complex, but the overall picture is one of a major, long-term reduction in broadleaved trees (Björse and Bradshaw 1998, Lindbladh et al. 2000, Nilsson et al. 2005, Lagerås 2016), especially old broadleaves (Axelsson and Östlund 2001) and oaks (Lindbladh and Foster 2010). The picture for oaks since the 1950s is especially complex, with an increase in standing volume in southern Sweden resulting from forest regrowth, but a decrease in oak regeneration and a steep decline in open wood pastures conducive to old, large oaks (Petersson et al. 2019).

1.5 Managed and unmanaged forests

Managed forests are here taken to be those that are managed through forestry, for wood production. There are protected and other conservation forests that are also managed (e.g. through methods such as those used in **Paper I**), but for the sake of simplicity, I am here contrasting managed production forests to forests that are primarily treated with minimal intervention.

Around 8% of Sweden's forested area is formally protected (~6% of productive forest area, SCB [2021]), although much of this is in northern, alpine national parks. In the hemiboreal zone, less than 4% of the forested area is formally protected (Constantino and Eriksson 2019). Beside formally protected areas, to the area of forest not managed for forestry can be added voluntary set-asides (~4% of forest area), general conservation considerations (~1.5%) and forests that produce less than one cubic meter of wood per ha and year (i.e. low-productive forests, which are to some extent formally protected, ~12%, Constantino and Eriksson [2019]). Among the voluntary set-asides are Woodland Key Habitats, small forest stands registered by the Swedish Forest Agency or major forestry companies. These are designated as important for biodiversity and are exempt from forestry through PEFC (Programme for the Endorsement of Forest Certification) and FSC (Forest Stewardship Council) certification (PEFC 2017, FSC 2020). Since the 1990s, more than 100,000 Woodland Key Habitats have been registered in Sweden (Gustafsson and Hannerz 2018). However, they have recently become the subject of much debate, with further registration now halted. Although they are generally small (on average 4.6 ha in Sweden, Timonen et al. [2010]), affected by edge-effects (Aune et al. 2005), and often with a history of partial cutting (Jonsson et al. 2005, Jönsson and Jonsson 2007), the general scientific consensus is that they are an important part of forest conservation in Fennoscandia, with a generally higher occurrence of red-listed species than production forests (Gustafsson and Hannerz 2018, Häkkilä et al. 2021).

Most of the roughly 80% remaining forest area is managed for production through highly efficient, almost exclusively even-aged, clear-cutting forestry (Felton et al. 2020). About half of this is done through small-scale, private ownership and the other half by large forestry companies (Barklund 2009). There is a clear gradient of decreasing small-scale private ownership going from the south (study regions in this thesis) towards mid- and northern Sweden, where state and private forest companies own nearly all forest land (Felton et al. 2020). Most of Fennoscandian forestry is based on Norway spruce or Scots pine, with these species making up about 40% each of the basal area in Swedish forests. Birches are the third most common at around 13%, with the remaining tree species all under 2%. In southern Sweden (Götaland), oaks make up 4.2% (Nilsson et al. 2021). For further details on forest composition in Götaland, see Götmark et al. (2005).

Spruce-dominated Fennoscandian production forests typically go through a similar set of successional stages and management interventions. After final harvest the (almost clear-cut) land area is treated by soil scarification (Nyland 2016) to favor growth of planted spruce (Fig. 4a). Shelterwood (scattered seed trees) of conifers may be left (Karlsson et al. 2017), as well as retained tree groups or single trees. Dead wood is present in the form of stumps, logging slash and retention wood (primarily high stumps). If the forest was previously unmanaged, there are possible “biological legacies” of a type that may not be created again during the new forestry regime, e.g. large diameter logs (Franklin et al. 2000). As the area is sun-exposed, pioneer species such as birch establish and grow up in competition with the planted spruce (Fig. 4b). A pre-commercial thinning is performed 5-15 years after planting (Fig. 4c). Here, competitors are cut, but the wood is left at the site (Pettersson et al. 2012, Sveaskog 2015). Dead wood is created in the form of fine diameter stumps and stems, often of birch. Then follows a relatively long period without intervention, as spruce grows and the canopy closes (Fig. 4d). Dead wood is relatively sparse, unless stands start to self-thin. Trees other than spruce are present to the extent they have been left as retention and have survived competition. At around 25-30 years, commercial thinning is performed (Fig. 4e). This may be the last thinning before final harvest, or several commercial thinnings may occur depending on stand conditions. Selected trees (spruce, but also some broadleaves, mainly birch) are cut to improve growth before final harvest. As the thinning is commercial, cut stems are removed from the stand (Agestam 2015). Dead wood is left as logging slash and stumps, primarily of spruce, and some birch. After 60-70 years (varying depending on productivity, longer in the north), the stand is ready for final harvest again (Fig. 4f). At this point, dead wood is again relatively sparse. In 2017-2018, 265,000 ha of forest were pre-commercially thinned in Sweden, 316,000 ha were commercially thinned, and 202,000 ha were final harvested (Nilsson et al., 2019).

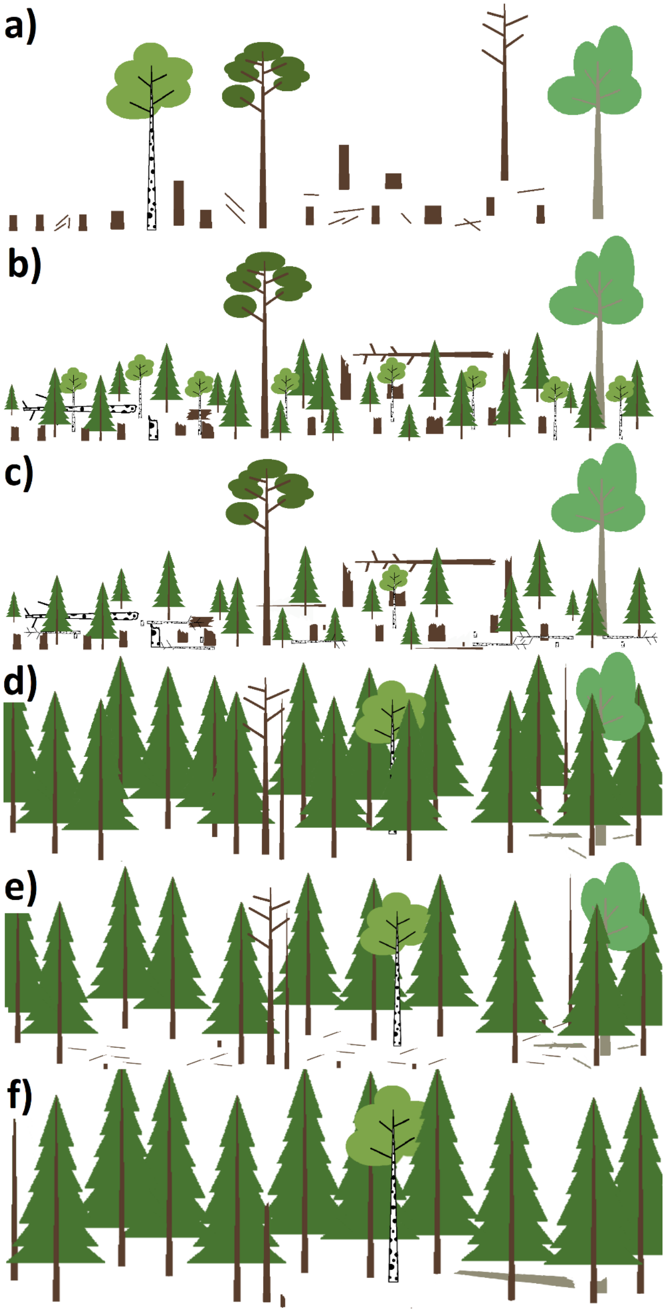

Figure 4. Schematic overview of the lifecycle of a typical spruce production forest. See main text for details. a) Soon after final harvest b) 5-15 years c) pre-commercial thinning d) 25-30 years e) commercial thinning f) ~70 years, soon before final harvest.

As the above outline indicates, deadwood recruitment in managed stands is highly varied over time, largely following management interventions (McCarthy and Bailey 1994, Sippola et al. 1998, Ranius et al. 2003, Montes and Cañellas 2006, Brin et al. 2008, Duvall and Grigal 2011). Swedish production forests contain on average around 7.5 m^3/ha of dead wood (Jonsson et al. 2016), with more on average in northern forests (~10 m^3/ha) than e.g. in the hemiboreal zone (~3.5 m^3/ha, Fridman and Walheim [2000]). Note that most studies do not include fine woody debris (<10 cm diameter), a dead wood type common e.g. after thinning (Siitonen 2001), and possibly representing high volumes (Nordén et al. 2004). The diversity of dead wood is generally low in managed forests, consisting primarily of lying dead wood, small diameters (<20 cm), early decay stages and coniferous species (Sippola et al. 1998, Siitonen 2001, Gibb et al. 2005, Brin et al. 2008, Duvall and Grigal 2011, Jonsson et al. 2016). Coarse dead wood is rare (McCarthy and Bailey 1994, Fridman and Walheim 2000) and may be damaged by logging operations (Hautala et al. 2004, Rabinowitsch-Jokinen and Vanha-Majamaa 2010). Trees with cavities are also rare (Andersson et al. 2018).

Succession in unmanaged forests is more varied than in managed forests, following several complex alternative pathways depending on type of disturbance, site factors, and plant species (Yearsley and Parminter 1998, Perry et al. 2008, Kuuluvainen 2009). Disturbances at varying intensities and scales include self-thinning, natural senescence, drought, insect attack, windthrow, flooding, and fire (Esseen et al. 1997, Kuuluvainen 2009, Stokland et al. 2012). Disturbances at the scale of a single tree are often called gap dynamics (Kuuluvainen 1994, Esseen et al. 1997, McCarthy 2001), and create small-scale heterogeneity and complexity. Large-scale disturbances such as fires are often followed by a biologically rich broadleaf-phase (Esseen et al. 1997).

Reported average amounts of dead wood in natural unmanaged forests vary greatly, from 50-120 m^3/ha for Fennoscandian boreal forests (Siitonen 2001), up to 350 m^3/h for some central European old-growth forests (Lachat and Müller 2018). Woodland Key Habitats in Sweden average around 20 m^3/ha of dead wood (Gustafsson 2001), significantly higher than average production stands (Timonen et al. 2011). Dead wood recruitment in unmanaged forests is highest in young stands after disturbance, and in old-growth stands due to natural senescence (Yearsley and Parminter 1998, Siitonen 2001), but the recruitment is more gradual than in managed forests (Stokland et al. 2012). The diversity of dead wood is high in unmanaged, semi-natural and natural forests (Stokland et al. 2012, Shorohova and Kapitsa 2015), with many snags and dead trees, coarse dead wood, advanced decay stages, and tree cavities (Siitonen 2001, Nilsson et al. 2002, Rimle et al. 2017, Andersson et al. 2018). One review estimated the dead wood diversity in Woodland Key Habitats to be more than 60% higher than in production stands (Timonen et al. 2011). The dead wood diversity of unmanaged stands is likely caused by the overall higher structural and compositional complexity (Kuuluvainen 2009), and the continuous recruitment of dead wood (Seibold and Thorn 2018).

1.6 Previous research on diversity differences

The traditional view of Fennoscandian boreal forests was that they are adapted to large-scale, stand-replacing disturbances (mainly fire) leading to even-aged dynamics. This has in turn been used to argue that even-aged clear-cutting forestry is a suitable management method to replace these natural disturbances, benefitting forest biodiversity (Berglund and Kuuluvainen 2021). Indeed, several studies have found a relatively rich fauna of saproxylic beetles on clear-cuts, including red-listed species (Kaila et al. 1997, Martikainen 2001, Jonsell and Schroeder 2014, Rubene et al. 2017). However, the idea that clear-cutting is a functional replacement for natural disturbances such as forest fires has also been heavily criticized, from two primary perspectives. The first argues that there is an inevitable trade-off between forestry and biodiversity, as the former strives for simplification and rationalization while the latter requires heterogeneity and complexity (Brockerhoff et al. 2008). On a more basic level, forestry and saproxylic organisms both compete for the same resource (the wood itself), which during clear-cutting, unlike during a natural disturbance, is removed from the forest (Lindenmayer and Franklin 2002, Jonsson et al. 2005, Perry et al. 2008). The second criticism stems from the new view of natural Fennoscandian boreal forest disturbance dynamics outlined in the earlier section. Under this view, these systems and the species therein are not adapted primarily to stand-replacing disturbances but to multi-scaled and primarily small-scaled disturbances. Given this, the even-aged clear-cutting model will be a poor fit to mimic these dynamics (Kuuluvainen 2009, Kuuluvainen et al. 2012, Berglund and Kuuluvainen 2021).

Several attempts to evaluate the diversity differences between managed (for production) and unmanaged forests have been done since the 1990s, with varying results. A 2010 meta-analysis found a significant medium-sized negative effect of management on saproxylic beetles in Europe (Paillet et al. 2010b). The meta-analysis included 17 studies of saproxylic beetles, but was criticized for using pseudoreplicated studies and for an overuse of studies based solely on bark beetles, among other things (Halme et al. [2010], response in Paillet et al. [2010a]). A 2011 meta-analysis of biodiversity differences between Woodland Key Habitats and production forests in Fennoscandia found more species in the former for all studied groups except saproxylic beetles (Timonen et al. 2011). A 2016 meta-analysis found a non-significant negative effect of clear-cutting forestry on arthropods, both globally and in Europe (Chaudhary et al. 2016). Two 2021 meta-analyses on the response of beetles (i.e. not saproxylic beetles specifically) to plantation forestry (i.e. not necessarily entirely analogous to most forestry in Fennoscandia, although the definition of plantation forestry is debated) found negative effects in the tropics, but none in European forests with native trees (Albert et al. 2021, López-Bedoya et al. 2021).

Some statistical and methodological problems are common to many of the studies comparing saproxylic beetle diversity between managed and unmanaged forests. Several of them have low sample sizes, or suffer from pseudoreplication with many traps within the same forest treated as statistically independent. Most of the studies focus exclusively on local diversity, while relevant differences may manifest at larger scales. Commonly they treat saproxylic beetles as one monolithic group, likely missing nuances resulting from widely varying ecology between species, or at the other end of the spectrum focus on one or two non-representative beetle families. Some common management stages, like pre-commercial thinning, have seen considerably less attention than e.g. clear-cuts.

Properly evaluating the degree to which saproxylic beetles can utilize managed production forests is important for at least two reasons. Firstly, it will inform us of an important environmental impact of current forestry practices and may indicate the need to change these practices if biodiversity targets are to be met. Secondly, it will provide important information on the distribution and preferences of saproxylic beetle species. This in turn should inform conservation management and red-listing.

2 Research aims

The overall aim of my thesis is to evaluate how the diversity of saproxylic beetles is influenced by type of management (production- or conservation-oriented active management or no active management) in forests of several different kinds (broadleaf-dominated or coniferous; early- or late-successional) and at different geographical scales in the hemiboreal zone of south-central Sweden. The main aims of the four papers are as follows:

Paper I: test the 10-year effect of conservation-oriented thinning contrasted with minimal intervention on the diversity and composition of saproxylic oak beetles in oak-dominated forests.

Paper II: evaluate the difference in saproxylic beetle diversity and composition between recently pre-commercially thinned young spruce production stands and mixed broadleaf-dominated Woodland Key Habitats.

Paper III: evaluate the difference in saproxylic beetle diversity and composition between recently commercially thinned middle-aged spruce production stands, unthinned middle-aged spruce production stands, spruce-dominated Woodland Key Habitats and spruce-dominated nature reserves.

Paper IV: evaluate the influence of characteristics of forests in the surrounding landscape on the local diversity of saproxylic beetles in managed and unmanaged forest stands within a spruce production forest context.

3 Study designs and methodology

3.1 Study designs

All four papers in this thesis use a study design of geographically paired stands, representing differing managed or unmanaged forest types. **Paper I** differs in being based on an experimental setup focused on conservation-oriented management in oak forests in southern Sweden, while the other three papers are observational, in a hemiboreal Swedish spruce production forest context.

3.1.1 Paper I

The paper is part of the Swedish Oak Project (Götmark [2013], gu.se/en/research/the-swedish-oak-project), a long-running research project comparing conservation management alternatives for mixed oak forests in southern Sweden. In a robust Before-After, Control-Impact (BACI) design, 25 pairs of 1 ha, mixed, oak-dominated forest plots throughout southern Sweden were selected in 2000. One plot in each pair was randomly designated as experimental plot, and the other as reference plot. The plots were either Woodland Key Habitats or reserves (i.e. largely unmanaged), and all had a similar history of being part of the open, grazed, pre-industrial agricultural landscape, turning into closed-canopy woodland through 20th century regrowth. A number of species groups and forest characteristics were surveyed in each plot, before experimental management took place in the experimental plots in the winter of 2002/2003. The experimental management consisted of conservation-oriented thinning with the aim to benefit oaks, in which around 25% of the tree basal area was removed (mainly competitors to mid-sized and larger oaks, such as spruces). In the years directly following the thinning, species groups and forest characteristics were resurveyed in both plots in each pair, and the effect of the thinning was evaluated. Beetles were surveyed on 22 out of the 25 sites, in 2001 (before thinning) and 2004 (shortly after thinning), published in Franc and Götmark (2008). See that paper for further details on methods and early results.

Paper I consists of a longer-term follow-up to this initial study, using 8 of the 22 sites. This follow-up took place 10 years after the thinning, in 2013, and used a selection of sites representative both of the geographic distribution throughout southern Sweden, and the range of regrowth in the experimental plots. Both data from the initial 2001-2004 sampling and the new 2013 sampling were used (Fig. 5). As the 2008 study also analyzed effects on herbivore beetle species (non-saproxylic species living on green parts of plants), these were also included in the follow-up.

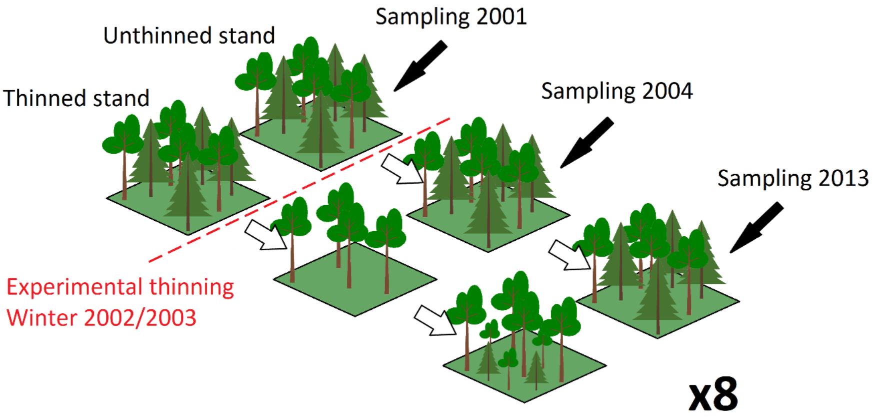

Figure 5. Study design for **Paper I**, schematically illustrating one of 8 pairs of plots

3.1.2 Paper II

This paper compares the saproxylic beetle diversity between one managed and one unmanaged forest type, sampled in May-June 2015. Ten pairs of forest stands in south-central Sweden (roughly Jönköping county) were used, each pair consisting of a young (~10-15 years), planted spruce production forest newly subjected to pre-commercial thinning, and one mixed, broadleaf-dominated Woodland Key Habitat within 2.5 km. The Woodland Key Habitats were chosen to be broadleaf-dominated to match the dominance of birch dead wood in the production stands following pre-commercial thinning. All stands were owned by the state forest company Sveaskog, and stand selection was done using their database.

3.1.3 Paper III

This paper uses a similar design to **Paper II**, comparing the saproxylic beetle diversity of two managed and two unmanaged forest types. Sampling took place over two years (May-July 2017 and 2018) and in two different regions (Jönköping, same as **Paper II**, and roughly Örebro county). In Jönköping 2017, 10 pairs of forest stands were used, each pair consisting of a middle-aged (~35-50 years), planted spruce production forest newly subjected to commercial thinning, and one spruce-dominated Woodland Key Habitat within 2.5 km. Additionally in Jönköping, three spruce-dominated old-growth nature reserves were used, not paired with any other stands. In Örebro in 2018, 10 triplets of stands were used, consisting of one commercially thinned stand and one Woodland Key Habitat like the ones in Jönköping, with the addition of a middle-aged spruce production stand that had not yet been subjected to commercial thinning. Beyond expanding the stands available for study, the inclusion of a second study region allowed for potential contrasts between the regions. Jönköping county is a heavily managed region with very few old, unmanaged forests, while Örebro county has a higher proportion of Woodland Key Habitats. Once again, all stands in this paper were owned by Sveaskog, except the three nature reserves sampled in 2017.

3.1.4 Paper IV

This paper uses the combined data from **Papers II-III** (73 stands) to look at the influence of the surrounding landscape on the diversity of saproxylic beetles. While **Paper II** only included samples from May-June 2015 due to time constraints, **Paper IV** added samples collected in July, to allow comparability with the 2017-2018 May-July sampling. Four forest landscape variables were calculated based on map data (amount of broadleaf forest, amount of forest over 100 years, amount of conservation forest, amount of clear-cut), at three spatial scales (within 250, 1250, and 2500 m).

3.2 Sampling methodology

All four papers use the same basic sampling methodology based on two flight-interception traps (also known as window traps) per plot or stand. Flight-interception traps consist of a clear plastic sheet suspended vertically above an open container filled with preserving liquid (glycol). Flying beetles collide with the sheet or otherwise fall into the container, drowning them, allowing for effective passive sampling during the flight-period (primarily May-July).

3.2.1 Paper I

This paper uses sampling methodology mimicking that in Franc and Götmark (2008) to allow proper comparisons between the years. Clear plastic panes, 600 cm^2 in size, were placed vertically directly against dead oak trunks, with a white plastic container underneath. Two traps per plot were used, one on a recently dead tree and one on an older dead tree, to better characterize the fauna of the plots.

This variant of flight-interception trap is widely used in species surveys of saproxylic beetles, as they are easy to attach directly to the substrate and generally catch a high proportion of beetles of interest to conservation.

3.2.2 Papers II-IV

The sampling for **Papers II-IV** all use the same methodology, with two flight-interception traps of the model IBL-2 (CHEMIPAN, Warsaw) per forest stand, suspended between living trees. The IBL-2 traps are commercially made traps for surveys of forestry pest insects (primarily bark beetles), also widely used in scientific sampling of other saproxylic beetles. They consist of a roughly 3,000 cm^2 clear triangular plastic sheet suspended between two plastic gutters and a plastic roof, forming a downward-facing triangle. At the bottom of the triangle is a funnel leading to a collection bottle.

3.3 Statistical methodology

The papers look at differences in both species diversity and composition, using an overall similar statistical framework.

For univariate measures of diversity, I have used the ‘number of species’ (i.e. species richness or species density). While a myriad of species diversity indices exist, many taking species evenness into account in different ways (Magurran 2013), I have chosen to use number of species as it is a straightforward measure that facilitates interpretability. To complement this diversity measure, I have also included rank abundance curves as a simple illustration of evenness in **Papers I-III**.

The terms species richness and species density are often confused. When species are sampled within a specified area (such as the area sampled by a trap), the measure is most properly called species density (Gotelli and Ellison 2004). However, the term species richness is used more commonly (but often incorrectly), so to avoid confusion I have tended to use the more general *species diversity* in this thesis.

Species diversity can be measured at several different scales, and in this thesis I have utilized the framework of alpha (α), beta (β), and gamma (γ) diversity (Whittaker 1960, Gotelli and Ellison 2004, Socolar et al. 2016) to differentiate between these scales (Fig. 6).

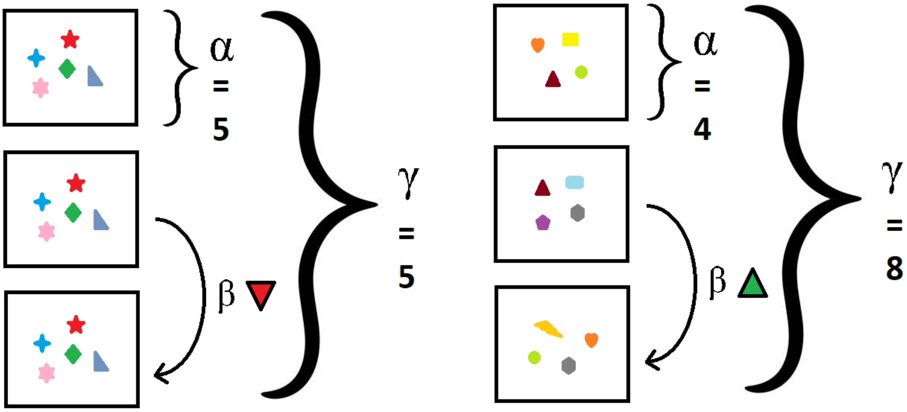

Figure 6. Schematic illustration of alpha (α), gamma (γ), and beta (β) diversity. Squares represent sample plots and colored shapes represent different species found in the plots. The three plots on the left have higher alpha (per-plot) but lower beta (compositional) and gamma (total) diversity than the three plots on the right.

3.3.1 Alpha diversity

The average species diversity per sampling unit is called alpha diversity. In my papers, this is the number of species per plot or stand (**Paper I** and **Paper IV**) or per trap (**Papers II-III**).

The geographically paired nature of my study designs means that sampling units are not independent, violating a core assumption of many statistical models and leading to potential pseudoreplication. To deal with this, I have used mixed models to test for differences in alpha diversity. These models account for statistical dependence by adding a random factor, corresponding to the geographic clustering of sample points.

For **Paper I**, I used linear mixed models (LMMs) to test the difference between the three sampling years (categorical) in average alpha diversity of the experimental plots relative to the reference plots. In other words, the model estimates should be interpreted as the average difference in the number of species between an experimental plot and the corresponding reference plot (experimental minus reference). Statistical significance of the intercept (year 2001) is interpreted as the difference between the plot types being statistically different from zero before the thinning, while statistical significance of the other two years (2004 and 2013) is interpreted as the difference between that year and 2001 being statistically significant. I further used a separate LMM to test the influence of local environmental (continuous) variables on alpha diversity in 2013. For these, estimates are interpreted as the change in the number of species per unit of the environmental variable.

For **Papers II-III**, I used generalized linear mixed models (GLMMs) to test the difference in average alpha diversity between forest types and regions (categorical). GLMMs are an extension of LMMs allowing for alternative data distributions (Bolker 2015), such as the Poisson distribution, which is often more appropriate for count data than a normal distribution would be (Gotelli and Ellison 2004). For these models, estimates are deviations of the specified level of the variable from a pre-determined reference (for forest type, this is Woodland Key Habitats), expressed as odds ratios. In other words, a value below 1 indicates lower alpha diversity relative to the reference and a value above 1 indicates higher diversity. Statistical significance indicates a statistically significant difference from 1, i.e. the reference level. I further used GLMMs to test the influence of local (**Papers II-III**) and landscape (**Paper IV**) environmental (continuous) variables on alpha diversity. For these, the estimates are interpreted as the proportional change in the number of species per unit of the environmental variable.

3.3.2 Gamma diversity

The combined species diversity of all sampling units is called gamma diversity. In my papers, this is the total number of species for all plots or stands of one forest type.

I have used species accumulation curves to compare gamma diversity between forest types in **Papers I-III**, as these are robust and informative (Gotelli and Colwell 2001). They plot the excepted number of species against the number of sampling units, from 1 to n using rarefaction, and for values higher than n through extrapolation. The plots are informative in three main ways. The species diversity at the end of the curve is the gamma diversity, i.e. the combined diversity of all sampling units. Non-overlapping 95% confidence intervals between curves representing different forest types indicate significant differences in gamma diversity. The confidence intervals are conservative, meaning that a lack of overlap indicates statistical significance, but the opposite is not necessarily true (Colwell et al. 2012). Furthermore, rarefaction allows for comparisons between samples of different sizes, e.g. between the nature reserves (n=3) and thinned stands (n = 10) in **Paper III**. In other words, it allows you to tell what the diversity of the larger sample would have been if limited to the sample size of the smaller sample. At the same time, extrapolation based on an asymptotic species richness estimator using the incidence of singleton (occurring once) or doubleton (occurring twice) species allows the effective sample size to be increased, giving an estimate of the richness of the community closer to complete sampling (i.e. true gamma diversity). Lastly, the slope of the curves indicates the degree to which the species community has been thoroughly sampled. A curve which is still steeply increasing towards the end means that each additional sampling unit would be likely to find many new species, while a flattening curve indicates that most of the species have been found.

The measures of alpha and gamma diversity are relatively straightforward, and the differences between them are only a matter of relative scale. A hypothetical study could treat the number of species sampled by individual traps in a forest stand as alpha diversity and the combined species sampled by all traps in the forest stand as gamma diversity. If the scale of the study was to increase to include several different forest stands, the combined species sampled by all traps in a forest stand (previously gamma diversity) would now instead be seen as alpha diversity, and the combined species sampled in all forest stands would be gamma diversity.

3.3.3 Beta diversity and species composition

As I have used it, beta diversity is the average degree of change in species composition from one sample unit to another within a category. Beta diversity mediates between alpha and gamma diversity. As seen in the example in Figure 6, although the three plots on the left have higher alpha diversity, their low beta diversity means they have lower gamma diversity than the three plots on the right (in this unrealistic example $\beta = 0$ and $\alpha = \gamma$ for the plots on the left). In other words, no extra species are added to the total (gamma) diversity by adding plots to the sample, as each plot contains the same species. In its simplest original form, beta diversity is the ratio of gamma to alpha diversity, $\beta = \gamma/\alpha$ (Whittaker 1960). Since then, a myriad other measures of beta diversity have been proposed, and there is no agreed-upon best measure (Tuomisto 2010, Anderson et al. 2011). I have used multivariate dispersion as a measure of beta diversity, with differences tested using the permutational method PERMDISP (Anderson 2006). The multivariate distances analyzed by PERMDSIP are based on a chosen dissimilarity measure, each of which will give different weight to species abundances. In my papers, I have used Bray-Curtis, Modified Gower, and Sørensen dissimilarity, the first two of which are abundance-based, and the latter incidence-based. Multivariate dispersion based on a distance measure that takes species abundances into account is not strictly speaking measuring beta diversity, as this has traditionally only taken into account presence-absence of species (Anderson et al. 2011). I nonetheless use the term beta diversity, as 1) the term is much better known than multivariate dispersion and fits into the framework of alpha-beta-gamma and 2) it measures much the same thing, i.e. variability in species composition.

For testing differences in species composition between the forest types, I have used PERMANOVA (Anderson 2001). Like PERMDISP, this is a permutational method that uses a chosen dissimilarity measure, but which does so in an ANOVA-style variation partitioning. PERMANOVA tests for differences in both multivariate dispersion (like PERMDISP) and location, i.e. species composition. A significant result in a PERMANOVA means that there are differences in either species composition, beta diversity, or both. A significant PERMANOVA in combination with a non-significant PERMDISP confirms differences in species composition, but if both are significant further investigation is required to determine the nature of the differences, e.g. through an ordination plot (Anderson and Walsh 2013).

In an ordination plot, multivariate data is reduced to two (sometimes three) dimensions, each of which contains as much of the variation in the original data as possible. In my papers, I have used non-metric multidimensional scaling (NMDS), a robust ordination technique that can use the same dissimilarity measures as the analyses above (Gotelli and Ellison 2004). From a dissimilarity matrix of all sample points, the NMDS tries to place these in two-dimensional space in such a way that the relative distances are preserved, i.e. points should be closest to the least dissimilar points, but absolute distances are not preserved. The degree to which this cannot be achieved is expressed as the stress-value of the NMDS.

Differences in species composition (multivariate location) can be seen by the degree to which there are distinct, non-overlapping groups of points for different categories, e.g. forest types. If groups of points from different categories do not overlap, this indicates that the categories contain different species communities, while overlap indicates no clear differences. Note that NMDS gives a qualitative, not quantitative view of differences, as relative, not absolute, distances are preserved. Beta diversity (multivariate dispersion) can be seen by the degree to which points within a category are spread out or clustered. A category in which the points are spread out from each other indicates that the sample points are not as similar to each other in terms of species composition as points in a category where they are tightly clustered, i.e. beta diversity is higher in the first case. The PERMDISP analysis is directly testing this, measuring the average distance of points in a category from the centroid of all points in the category.

4 Summary of main results

The total sample from **Papers I-IV** consists of 49,520 saproxylic beetle individuals belonging to 426 species and 45 families.

4.1 Paper I

This paper examines the 10-year effect of conservation-oriented thinning on saproxylic oak beetles and herbivore beetles in oak-dominated mixed stands, using a before-after control-impact design of eight geographically paired experimental and reference plots in southern Sweden.

There was a small and non-significant increase in the per-plot number of species (i.e. alpha diversity) in the experimental plots compared to the reference plots from before the thinning to shortly after the thinning, and a larger, significant increase after 10 years (p=0.007, Fig. 1). The increase in species in the experimental plots, controlled for by the increase in the reference plots, equaled around 33% from before the thinning to 10 years after. Note that Tables 2 and 3 in **Paper I** contain editing errors: Model 3 in Table 2 should say “Diff. in number of *herbivore* species”, and Model 4 in Table 3 should say “Number of oak saproxylic *species*”.

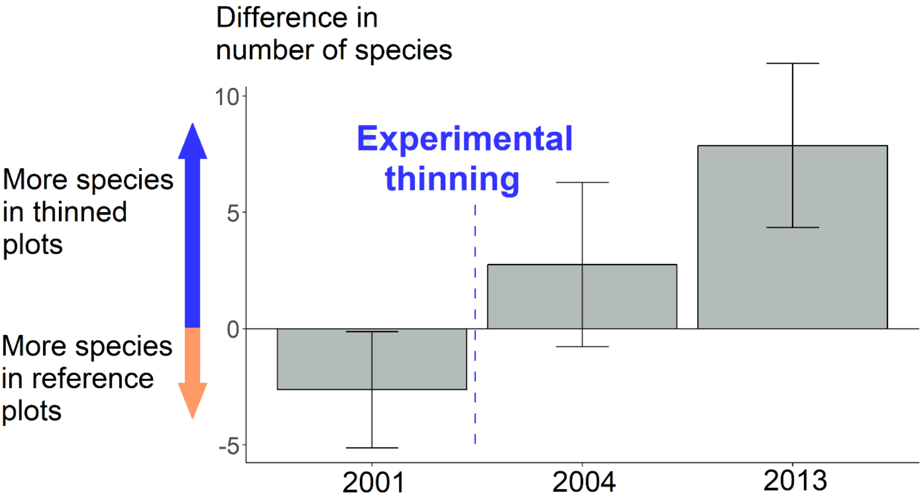

Figure 7. Average difference in per-plot number of saproxylic beetle species connected to oak (alpha diversity) between thinned experimental plots and unthinned reference plots. Positive values indicate higher diversity in thinned plots. The difference between 2001 and 2013 is statistically significant. n = 8. Error bars are SE.

In 2013, out of the local environmental variables ‘circumference of trap tree’, ‘volume of dead wood surrounding trap’, and ‘canopy openness around trap’, only the latter was significant (p=0.001), equaling around a 0.2 increase in the per-trap number of species for every percentage point increase in canopy openness.

The pattern for the total number of species (i.e. gamma diversity) was similar to that of the per-plot number of species, with a minor, non-significant difference between the plot types in 2004, and a larger, significant difference after 10 years, favoring the thinned stands (Fig. 8). There were no significant differences in species composition relating to the thinning.

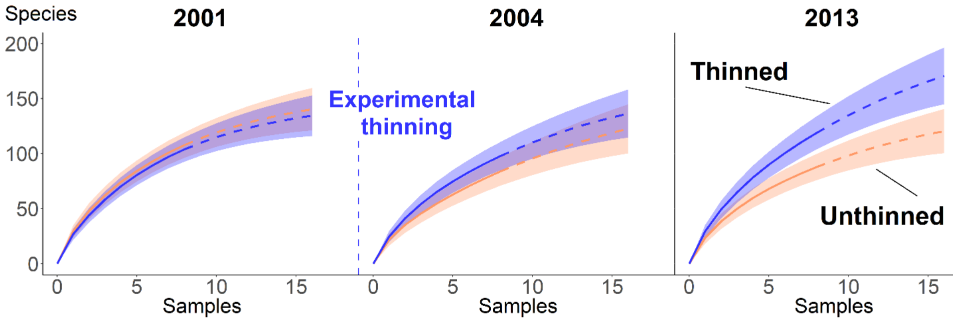

Figure 8. Species accumulation curves, showing an increase in total number of saproxylic oak beetle species (gamma diversity) in thinned experimental plots after thinning as compared to unthinned reference plots. Non-overlapping 95% confidence intervals indicate statistical significance. n = 8, extrapolated to n = 16 (dashed lines).

4.2 Paper II

This paper examines the difference in species diversity of saproxylic beetles between recently pre-commercially thinned young spruce production stands and mixed, broadleaf-dominated Woodland Key Habitats, using a design of 10 pairs of stands in southern Sweden.

There were no significant differences in the per-trap number of species (alpha diversity) between production stands and Woodland Key Habitats, for either saproxylic beetle species as a whole or red-listed saproxylic beetle species.

Among the local environmental variables ‘volume of dead wood around trap’, ‘diversity of dead wood around trap’ and ‘canopy openness around trap’, only the first was significant for saproxylic beetles as a whole (p=0.03), equaling around a 0.2% increase in the per-trap number of species per 1 m^3/ha increase in dead wood volume. The diversity of tree species and dead wood was higher in the Woodland Key Habitats, while the canopy openness and dead wood volume was lower.

Beta diversity of saproxylic beetles as a whole was higher in Woodland Key Habitats than in production stands (p=0.001), and there was a clear difference in species composition between the two types (p=0.001, Fig. 9).

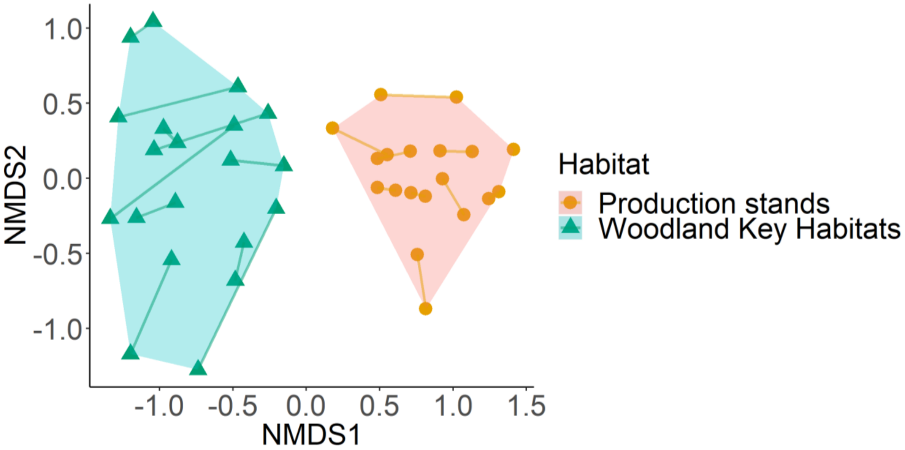

Figure 9. Ordination plot showing differences in species composition (multivariate location), as well as differences in beta diversity (multivariate dispersion) of saproxylic beetles between pre-commercially thinned young spruce production stands and mixed, broadleaf-dominated Woodland Key Habitats. Each point represents one trap, and traps in the same stand are connected by lines. Stress is 0.16.

The total number of species (gamma diversity) was similar between the forest types for saproxylic species as a whole, conifer-associated species, and predator species, but significantly higher in Woodland Key Habitats for red-listed species, broadleaf-associated species, and fungivore species. There were more wood consumer species in the production stands than in the Woodland Key Habitats, but the difference was not significant (Fig. 10).

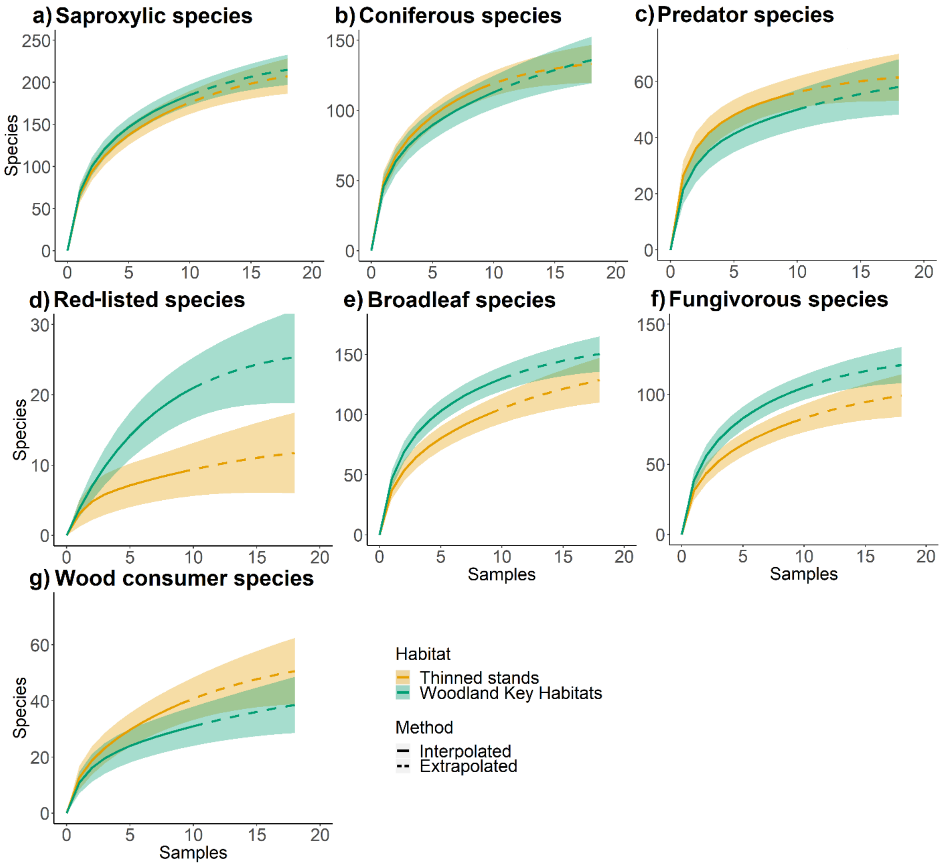

Figure 10. Species accumulation curves, showing differences in the total number of species (gamma diversity) between pre-commercially thinned spruce production stands and mixed, broadleaf-dominated Woodland Key Habitats, for saproxylic beetles as a whole (a), and six ecological groups (b-g). Non-overlapping 95% confidence intervals indicate statistical significance. n = 10, extrapolated to n = 20. (dashed lines).

4.3 Paper III

This paper examines the difference in species diversity of saproxylic beetles between recently commercially thinned middle-aged spruce production stands, unthinned spruce production stands, spruce-dominated Woodland Key Habitats and spruce-dominated nature reserves, using a design of 10 pairs of stands, 10 triplets of stands, and three reserves, in two regions in south-central Sweden.

There was a significant difference in the per-trap number of species (alpha diversity) between commercially thinned production stands and Woodland Key Habitats for saproxylic beetle species as a whole, with around 12% more species in thinned forest traps (lower 95% confidence interval = 1%, upper = 24%). There were no significant differences for the other forest types, or for red-listed saproxylic beetle species.

Among the local environmental variables 'volume of dead wood around trap', 'diversity of dead wood around trap' and 'canopy openness around trap', only the last was significant, for both saproxylic beetles as a whole (equaling around a 1% decrease in the per-trap number of species per percentage point of canopy openness, lower CI = 1%, upper = 8%) and red-listed species (equaling around a 2% decrease in the per-trap number of species per percentage point of canopy openness, lower CI = 1%, upper = 27%). The volume and diversity of dead wood and the diversity of tree species was higher in the Woodland Key Habitats than in the managed forests, while the canopy openness was similar.

Beta diversity of saproxylic beetles as a whole was higher in the Woodland Key Habitats than in the commercially thinned stands (p=0.015), but there were no clear differences in species composition between the forest types (Fig. 11).

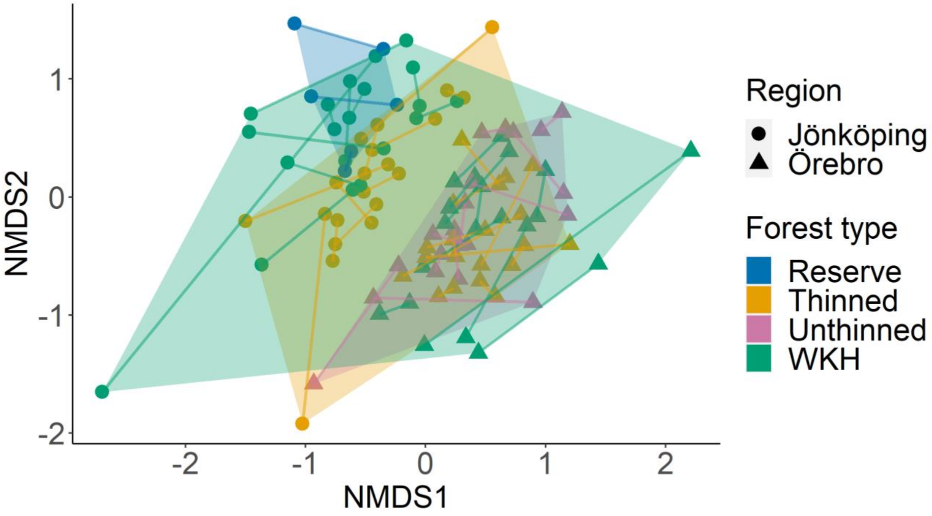

Figure 11. Ordination plot showing similarities in species composition (multivariate location), as well as differences in beta diversity (multivariate dispersion) of saproxylic beetles between two managed (thinned stands, unthinned stands) and two unmanaged (Woodland Key Habitats [WKH], reserves) forest types. Note that only thinned stands and Woodland Key Habitats were sampled in both regions, meaning that comparisons with the other types are unreliable. Each point represents one trap, and traps in the same stand are connected by lines. Stress is 0.24.

The total number of species (gamma diversity) was similar between the forest types for most species groups, but significantly higher in Woodland Key Habitats than in thinned stands for red-listed species in the region with more Woodland Key Habitats (Örebro), but not in the region with less (Jönköping, Fig. 12).

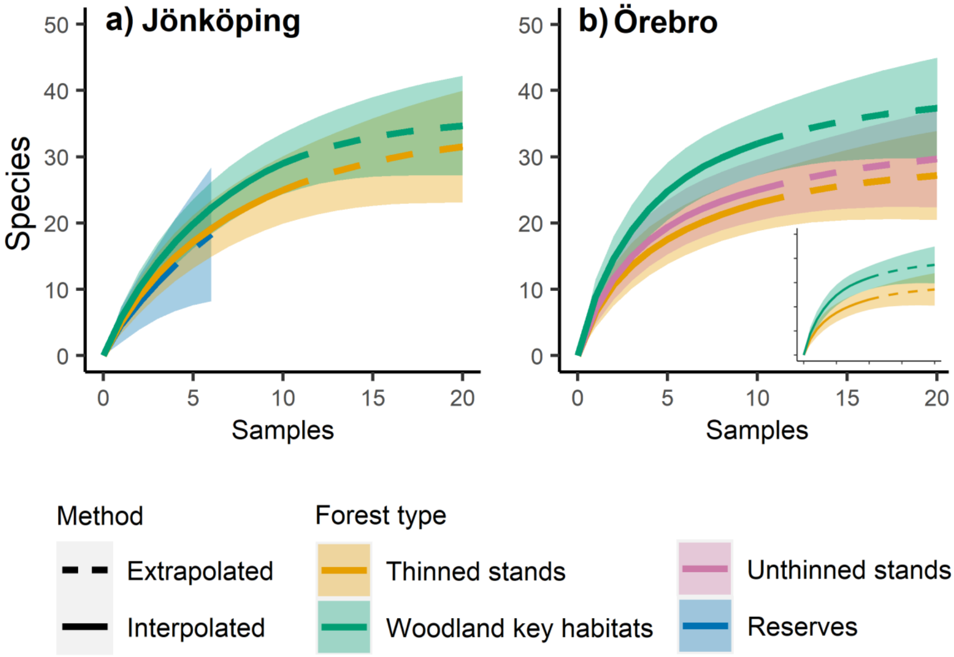

Figure 12. Species accumulation curves, showing difference in total number of red-listed saproxylic beetle species (gamma diversity) between commercially thinned spruce production stands, unthinned spruce production stands, spruce-dominated Woodland Key Habitats, and spruce-dominated nature reserves, in two regions with less (a) or more (b) Woodland Key Habitats. Non-overlapping 95% confidence intervals indicate statistical significance. n = 10, extrapolated to n = 20 for all forest types except reserves, where n = 3 extrapolated to n= 6 (dashed lines). The smaller graph in b shows the curves for thinned stands and Woodland Key Habitats with the unthinned stands removed for clarity.

4.4 Paper IV

This paper examines the influence of four landscape environmental variables (volume of broadleaved trees, area of forest over 100 years, area of conservation forest, area of clear-cut forest) at three scales (within a 250, 1250 or 2500 m radius) on the per-stand (alpha) diversity of saproxylic beetles in 73 stands in south-central Sweden, using the same data as in **Papers II-III**.

There was a positive association with broadleaved volume for saproxylic beetle species as a whole, equaling around a 0.7% increase in the per-stand number of species per m^3/ha of broadleaf volume, at a scale of 2500 m (Fig. 13, lower CI = 0.1%, upper = 2.3%). There was a similar but smaller association for fungivores, equaling around a 0.3% increase per m^3/ha of broadleaf volume, at scales varying between 250 and 2500 m (lower CI = 0.01%, upper = 0.7%). For all six forest types, there was a roughly equal number of species associated with broadleaf trees as with spruce.

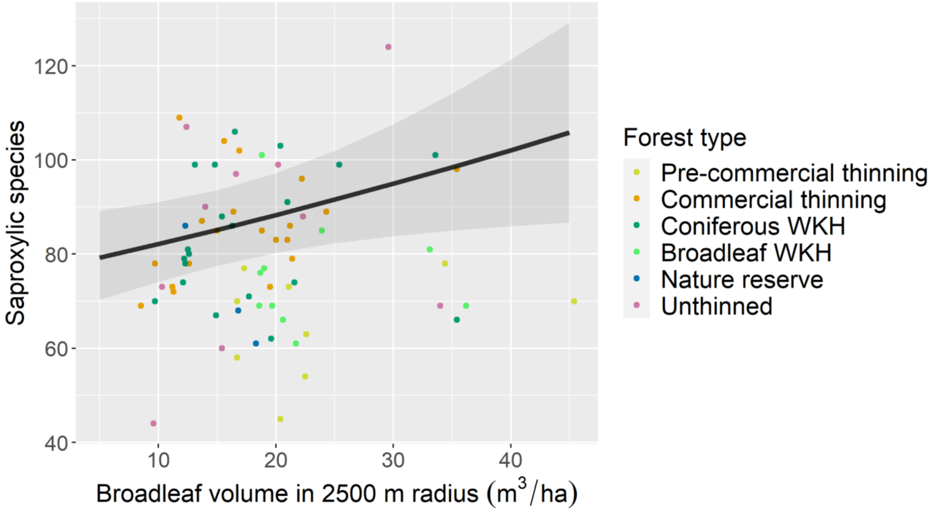

Figure 13. Marginal plot showing the association of per-stand number of saproxylic beetle species as a whole (alpha diversity) with broadleaf volume in the surrounding landscape, at a scale of 2500 m. Each point is one stand. Ribbon shows 95% confidence interval.

There was a smaller, negative association with forest over 100 years for red-listed saproxylic beetle species, equaling around a 0.3% decrease in the per-stand number of species per ha of old forest, at a scale of 2500 m (Fig. 14, lower CI = 0.1%, upper = 0.6%). There was a similar association for predators, equaling around a 0.2% decrease in the per-stand number of species per ha of old forest, at scales varying between 250 and 2500 m (lower CI = 0.05%, upper = 0.3%).

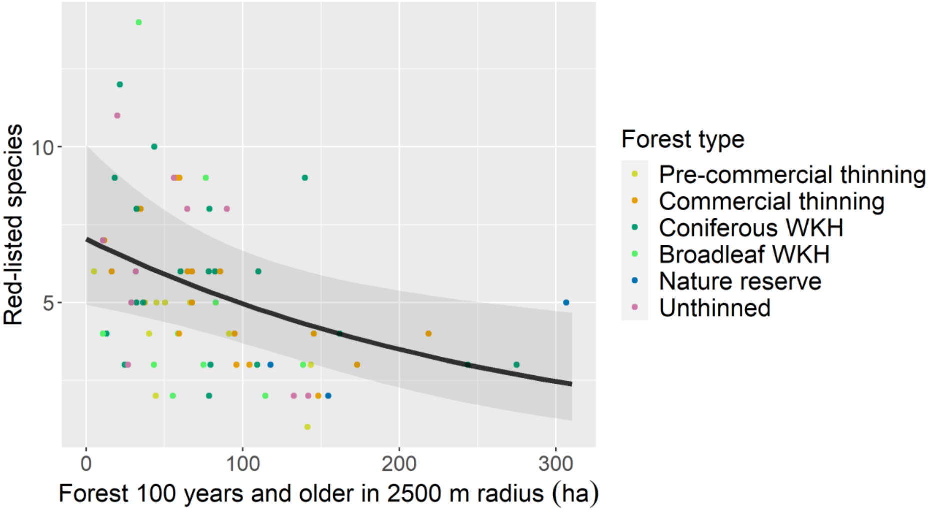

Figure 14. Marginal plot showing the association of per-stand number of red-listed saproxylic beetle species (alpha diversity) with area of old forest in the surrounding landscape, at a scale of 2500 m. Each point is one stand. Ribbon shows 95% confidence interval.

5 Discussion

5.1 Differences occur at scales larger than the local

For the observational studies of spruce production forests and Woodland Key Habitats (**Papers II-III**), I saw no differences in saproxylic beetle alpha diversity between the forest types, or higher diversity in managed stands. Although this may be surprising from a view of production forests as “ecological deserts” (Brockerhoff et al. 2008), it is in agreement with a number of earlier studies (see section 1.6). At the same time, Woodland Key Habitats had higher diversity at larger scales (beta and in some cases gamma). This is congruent with a general pattern of scale-dependence among many community ecology processes (Leibold and Chase 2017). It further matches a global picture of the effect of human influence on biodiversity, where local diversity remains unchanged or increases, while diversity at larger scales decreases (Niemelä 1997, Sax and Gaines 2003, Dornelas et al. 2014, Hillebrand et al. 2018, Primack et al. 2018, Chase et al. 2019). This pattern may be explained by the fact that local extinctions are balanced by increased dispersal of generalist species, such that local communities maintain the same number of species but the identities of those species increasingly become the same between communities (Leibold and Chase 2017). This process is known as biotic homogenization (McKinney and Lockwood 1999, Olden and Rooney 2006). If we assume that there are species associated with both managed production forests and unmanaged semi-natural forests, what pattern of diversity would we expect given the distribution of these habitats in southern Fennoscandia? With often small and fragmented unmanaged semi-natural forests dispersed in a landscape dominated by managed forests, unmanaged forest species will have a much harder time dispersing between stands than managed forest species. Given this pattern, and given the positive correlation between dispersal and local diversity (Vellend 2016, Leibold and Chase 2017), this would suggest that even if the unmanaged forest fauna as a whole is more species-rich, managed stands may end up with higher local diversity. Put differently, most species that can live in managed forests occur in every managed forest, while those associated with unmanaged forests are spread out among different stands.

Which scale of diversity is most relevant will depend on the reason for valuing biodiversity, which is often insufficiently considered in discussions of forestry. Alpha diversity may be most relevant if you are interested in ecosystem functioning, which often increases with local diversity (Leibold and Chase 2017). However, much of the debate around forestry in Sweden revolves around its impact on biodiversity trends, and our national and international commitments to preserve biodiversity. Here, diversity at larger scales (beta and gamma) is more relevant than the average local diversity of stands of a particular type.

5.2 Broadleaf diversity is important for saproxylic beetles

The value of broadleaf trees is a common theme in all four papers. Conservation–oriented thinning to benefit oak, often at the expense of spruce, had a clear positive effect on saproxylic oak beetles (**Paper I**). For several saproxylic beetle groups, gamma diversity was higher in broadleaf-dominated Woodland Key Habitats than in production stands, with no or weak differences between spruce-dominated Woodland Key Habitats and production stands (**Papers II-III**). Broadleaf forest in the surrounding landscape had a positive influence on saproxylic beetles (**Paper IV**).

Habitat and substrate heterogeneity is an important factor to the diversity of saproxylic beetles (Niemelä 1997, Stokland et al. 2012), and is an alternative explanation to the one outlined above for the higher beta diversity in the Woodland Key Habitats than the production stands. From the perspective of saproxylic beetles, managed spruce production forests likely come in only around four or five main distinct types, corresponding to successional stages (clear-cuts, the pre-commercial thinning stage, middle-aged unthinned or thinned stands, mature stands), within which the diversity of structures and substrates is low. In comparison, natural forests come in many forms, especially if the natural diversity of Fennoscandian tree species is allowed to manifest. It seems clear that an increase in the amount of broadleaved trees in Fennoscandian forestry would benefit forest biodiversity (Götmark et al. 2005, Brockerhoff et al. 2008, Felton et al. 2010, 2016, 2020, Bergquist et al. 2016). Similarly, within unmanaged forests, the importance of broadleaves needs to be emphasized. There is often a lack of representation of natural variability in protected areas (Nilsson and Götmark 1992, Baldi et al. 2017). Given that southern Fennoscandia was historically dominated by broadleaves and pine, from the perspective of saproxylic beetles it may be beneficial to give lower priority to old spruce forests in this region than to broadleaf forest when designating protected areas.

5.3 Woodland Key Habitats aid saproxylic beetle conservation

The beta diversity of saproxylic beetles was higher in Woodland Key Habitats than in productions stands (**Papers II-III**). For several beetle groups, including red-listed ones, gamma diversity was also higher in broadleaf-dominated Woodland Key Habitats than in the most broadleaf-rich production forest stage, the pre-commercial thinning stage (**Paper II**).

This is in agreement with the majority of previous research showing the conservation value of Woodland Key Habitats (Timonen et al. 2011, Gustafsson and Hannerz 2018), and small unmanaged habitat patches in general (Götmark and Thorell 2003, Ranius and Kindvall 2006, Wintle et al. 2019). However, I found the same (**Paper II**) or lower (**Paper III**) alpha diversity in Woodland Key Habitats as in production stands. The generally low diversity of the three reserves I sampled (**Paper III**) indicates that Woodland Key Habitats may be the best we have in terms of spruce-dominated unmanaged forests in the region. At the same time, Woodland Key Habitats are affected by edge effects (Aune et al. 2005) and previous management (Jönsson et al. 2009).

Furthermore, beside structural and substrate factors, they are selected based on indicator species primarily consisting of cryptogams (Timonen et al. 2010). A review of alpha diversity differences between Woodland Key Habitats and production forests found higher diversity in Woodland Key Habitats for all included groups (vascular plants, lichens, mosses, fungi) except saproxylic beetles (Timonen et al. 2011), and other studies have found that fungi used to indicate forest continuity do not correlate with the diversity of saproxylic beetles (Økland et al. 1996, Sverdrup-Thygeson 2001). It thus seems that although Woodland Key Habitats contribute to the diversity of saproxylic beetles at larger scales, potentially their selection criteria could be improved for this group.

5.4 The landscape matters for saproxylic beetles

The gamma diversity of red-listed beetles was higher in Woodland Key Habitats than in thinned stands in the region with a higher density of Woodland Key Habitats (Örebro) but not in the region with a lower density (Jönköping, **Paper II**). Furthermore, the amount of broadleaf forest in the landscape surrounding stands had a positive influence on saproxylic beetles as a whole and on fungivores, while the amount of old forest had a negative influence on red-listed beetles and predators (**Paper IV**). The surrounding landscape is clearly important for saproxylic beetles, in agreement with previous research (summarized in the discussion to **Paper IV**). The exact scale that is most relevant is hard to pinpoint, and will vary between species (Perry et al. 2008, Jackson and Fahrig 2012, Miguet et al. 2016). I found patterns within 2500 m from stands, but the results of **Paper II** indicate that scales much larger than that (i.e. between two separate study regions) may be important as well. It is important to point out that **Papers II-IV** all took place within landscapes with a long history of dominant spruce forestry. Extrapolation of results from landscapes highly affected by forestry to more untouched landscapes may not be appropriate (Perry et al. 2008), and previous studies have found contrasting responses of saproxylic beetles between more and less affected regions (Rubene et al. 2017, Larsson Ekström et al. 2021). The effects of forestry may manifest on a landscape level, by causing species sensitive to forestry to disappear regionally (Laaksonen et al. 2020). Comparisons between managed and unmanaged forests in such a region (perhaps partly like my study regions) may find no difference, and erroneously conclude that forestry does not negatively affect saproxylic beetle diversity. Such landscape-level differences may partly explain the general lack of difference in local diversity between managed and unmanaged stands in my studies, contrasted with differences found in similar studies in northern Sweden (Djupström et al. 2008, Stenbacka et al. 2010) and Finland (Martikainen et al. 2000).

It is also important to note that the influence of the surrounding landscape I found does not necessarily give support to the current focus on green infrastructure and landscape planning within Swedish forest conservation. The idea of green infrastructure (The Swedish Environmental Protection Agency 2022) is predicated on the notion that fragmentation is an important detrimental factor for forest species. As fragmentation per se and habitat loss in general are tightly linked and hard to disentangle (Fahrig 2003), the results may just as well give support to the idea that focus should be on the protection of as much high quality habitat as possible, rather than on the spatial configuration of that habitat (Komonen and Müller 2018).

5.5 Thinning affects saproxylic beetle communities

I found a positive, 10-year effect of conservation-oriented thinning on alpha diversity of oak beetles in oak-dominated stands (**Paper I**). I also found that commercially thinned spruce production stands had higher alpha diversity than Woodland Key Habitats, unlike unthinned stands, although gamma diversity did not differ (**Paper III**). These results are largely in agreement with previous research showing that thinning has a strong positive effect on saproxylic beetle species numbers (Maclean et al. 2015, Nadeau et al. 2015). However, many earlier studies have reported this effect to be short lived, gone or reduced already after a few years (Taki et al. 2010, Thibault and Moreau 2016, Gandiaga and Moreau 2019, Jokela et al. 2019, Koivula and Vanha-Majamaa 2020). These earlier studies have been done primarily in a coniferous, often spruce-dominated context similar to that of **Paper III**. This differs from the oak context in **Paper I** and could explain the contrasting, strong, longer-term effect found therein. Oaks and oak beetles are to a larger extent associated with open conditions (Lindhe et al. 2005, Bouget et al. 2014) while many spruce beetles may be adapted to stable conditions and closed canopy (Toivanen and Kotiaho 2010). Thinning should affect beetles in two separate ways. One is the initial resource pulse of dead wood, which seems to increase the number of saproxylic beetles regardless of forest type. The second is the longer-term influence of thinning on the structure and composition of the forest. In a spruce forest, the natural analogue of thinning (e.g. fire, windthrow, flooding) would usually be followed by a biologically rich broadleaf-dominated successional stage (Esseen et al. 1997). However, in a forestry context, this succession is suppressed to maintain spruce. In contrast, the conservation-oriented thinning in the oak forests was aimed at creating a more open habitat conducive to oaks in the long term, with thinned stands still more open than unthinned stands after 10 years. Additionally, for conservation management in conifer-dominated forests in the region, methods such as burning may yield better results for saproxylic beetles (Hjältén et al. 2017a, Hägglund et al. 2020).

Worth considering are also future climate change-driven effects on forests, with higher temperatures and summer droughts. Here, unmanaged, closed-canopy forest may have an important role to play as refuges, especially for coniferous forest species that may be especially sensitive to these changes (Evans et al. 2022). This role of unmanaged (or otherwise closed-canopy) forests warrants more scrutiny in the future.

5.6 What is being compared, and why?

The choice of comparison is crucial but perhaps insufficiently interrogated in studies of managed and unmanaged forests. **Papers II-III** illustrate two potential opposing problems. In **Paper II**, Woodland Key Habitats were chosen to be broadleaf-dominated.

Although this was done because the pre-commercially thinned production forests to which they were compared had much dead wood of birch, the Woodland Key Habitats still had a much higher diversity of broadleaf trees. Some may consider this an apples-and-oranges comparison, showing primarily the influence of broadleaf diversity on saproxylic beetles. In **Paper III**, Woodland Key Habitats were chosen to be spruce-dominated to match the spruce-dominance of the production stands. Here the criticism could instead be that the Woodland Key Habitats were not sufficiently representative of natural forests in the region, instead having been chosen to match the unnatural spruce-dominance that might be a primary reason why production forests are less diverse. There is no perfect comparison to be made between managed and unmanaged forests; instead the comparison hinges on the framework of questions within which it is made (Brockerhoff et al. 2008). One framework could be the desire to evaluate forestry against alternative land uses, such as letting the forests develop naturally. Here the comparison in **Paper II** may be most appropriate, with Woodland Key Habitats more representative of natural hemiboreal vegetation. Another framework could be the desire to evaluate Woodland Key Habitats as a tool for integrated conservation within Swedish forestry. Here the comparison in **Paper III**, with Woodland Key Habitats representative of many of those in south-central Sweden, may be most appropriate. A third framework could be the desire to identify species that seem to do poorly within managed forests, in which case both comparisons have their merits. All of these frameworks are valuable and part of the motivation for this thesis, but a more narrowed and specified framework might have yielded clearer results.

5.7 Capturing the ecological diversity of saproxylic beetles

For **Papers II-III**, I divided beetles into ecological groups (fungivores, wood consumers, predators, red-listed species) and found some contrasting, but mostly similar, responses. Even divided into ecological groups, it is still the case that all my results reflect the aggregate response of dozens or hundreds of species. If the species-specific responses are contrasting, the resulting average response may not be all that relevant (Koivula and Vanha-Majamaa 2020). This is a difficult trade-off. If one aggregates too much, contrasting individual responses and important patterns may be lost. If one subdivides the data too much, data dredging becomes a risk. If one avoids aggregating by focusing on a small subset of species, the results lose generalizability and relevance.

An important ecological division among the saproxylic beetles is between species associated with early, more open conditions and those associated with closed-canopy, later successions. Both of these groups are considered a priority within conservation (Tikkanen et al. 2006, Kuuluvainen and Gauthier 2018). However, it would seem that early-successional species should be easier to accommodate within the even-aged clear-cutting model of forestry, with sporadic pulses of dead wood and short rotation times. Uneven-aged forestry may be a viable alternative to support both early- and late-successional saproxylic beetle species, providing higher small-scale heterogeneity (Hjältén et al. 2017b, Joelsson et al. 2017, 2018).

For conservation, the response of red-listed species should be most relevant. Unfortunately, by dint of often being rare, these are very difficult to sample consistently (Martikainen and Kouki 2003, Martikainen and Kaila 2004). As a result, strong conclusions based on red-listed species are often difficult to draw. An interesting further use of the data in **Papers II-IV** would be to identify specific species strongly associated with either managed or unmanaged stands. Presumed rare or red-listed species found consistently in managed stands are likely to be overlooked, and may need reevaluation. Species consistently occurring in unmanaged stands, but seldom or never in nearby managed stands, may be good candidates for red-listing or conservation action.

I did not find clear differences in species composition between the spruce-dominated Woodland Key Habitats and production stands in **Paper III**. One potential explanation could be that the Woodland Key Habitats are surrounded by managed forest, with continuous dispersal of common generalist species into them. This potential dynamic, related to mass effects (Leibold and Chase 2017) and biotic homogenization discussed above, is interesting, but to my knowledge rarely studied within Fennoscandian forestry mosaics. Ås (1999) found more managed stand-associated species in small unmanaged stands than in large ones, indicating that such “invasions” may be happening in Woodland Key Habitats. In **Paper IV**, I found a negative influence of old forest and no significant influence of clear-cuts and conservation forest in the surrounding landscape, but the paper only considered alpha diversity. If biotic homogenization of Woodland Key Habitats due to dispersal from managed stands is happening, it should manifest at larger scales (i.e. beta diversity).

5.8 Are local factors important to saproxylic beetles?

I found overall weak and varied responses to environmental variables. There was a positive response to canopy openness in oak forests (**Paper I**), a positive response to dead wood volume in broadleaf-dominated Woodland Key Habitats and pre-commercially thinned stands (**Paper II**) and a negative response to canopy openness in spruce-dominated Woodland Key Habitats, reserves and production stands (**Paper III**). The contrasting responses to canopy openness in **Paper I** and **Paper III** match the contrasting ecology of oak- and spruce-associated faunas discussed in section 5.5 above.

In contrast to the lack of influence of dead wood volume in **Paper I** and **Paper III**, much previous research has found a positive effect (Seibold and Thorn 2018). A central European study found that the difference in saproxylic beetle diversity between historically managed and unmanaged forests disappeared after continuous dead wood addition in the former (Roth et al. 2018), indicating that this is a critical factor. The lack of influence of dead wood diversity in **Papers II-III** is also not in line with the majority of previous research (Seibold and Thorn 2018). This lack of influence could have several explanations. A few studies have found the effect of local dead wood volume to be dependent on the study landscape, or forest continuity (Brin et al. 2016, Rubene et al. 2017, Larsson Ekström et al. 2021), indicating that perhaps an influence would be seen if the study was repeated in a less heavily managed landscape. The fact that both dead wood volume and diversity were tested as averages over all forest types in each study may also have obscured contrasting effects between the forest types. Further, both measurements may not be properly capturing relevant aspects. Not all dead wood may be similarly valuable to saproxylic beetle diversity, and counting the aggregate volume of e.g. hundreds of small branches the same as that of one large log may be misleading. Similarly, measuring dead wood diversity is not straightforward, as it requires dividing dead wood objects into categories of equal relevance from the standpoint of saproxylic species. It may also be the case that the range of dead wood diversity was too low, especially in **Paper III** where all stands were spruce-dominated. Finally, it may be that the scale at which I measured environmental variables (~10 meters) is not the most relevant for influencing trap catches (Burner et al. 2021).

5.9 Pitfalls of saproxylic beetle sampling

All four papers utilize flight-interception traps for sampling saproxylic beetles. Overall these are very effective at sampling many species compared to other methods (Wikars et al. 2005), and this is especially true for the IBL-2 traps used in **Papers II-IV** (Burner et al. 2021). Despite this, there is likely to be large year-to-year variation in trap catches (Martikainen and Kaila 2004, Parmain et al. 2013), and as mentioned above it is especially difficult to consistently sample rare species (Martikainen and Kouki 2003, Martikainen and Kaila 2004). This being said, most of the species accumulation curves in the papers are starting to flatten, especially if considering the extrapolated data, indicating that at the very least most of the commoner species (i.e. most species) have been sampled.

A limitation of flight-interception traps that has been brought up is the fact that it is not possible to definitively connect the species caught to any particular habitat or substrate (Jonsson et al. 2005, Wikars et al. 2005). “Tourist” species that visit stands but do not end up colonizing may be especially prevalent after management interventions such as thinning (Gandiaga et al. 2018). Studies have both shown that flight-interception traps are sensitive to their immediate surroundings (Sverdrup-Thygeson and Birkemoe 2009), and the opposite (Burner et al. 2021). The effect of these possible “tourist” species will be to increase variance and make potential differences between habitats more difficult to detect. At the end of the day, this may be a necessary trade-off, as other sampling methods are considerably less effective, more labor-intensive, and miss large portions of species communities.

One potentially neglected problem with the widespread use of flight-interception traps in ecological research on saproxylic beetles is that they will, per design, preferentially sample species with higher dispersal ability. As dispersal ability is a central trait potentially influencing several other interconnected traits such as preference for early- or late-successional habitat, preference for sun or shade, tree species association, feeding biology, and sensitivity to forestry, fragmentation, and habitat loss (see section 1.3), the risk is that results will be biased towards the preferences of better dispersers.

A combination of methods, using flight-interception traps together with e.g. rearing of beetles directly from substrate, may give a more complete picture. More research concerning this and other methodological issues would be valuable.

6 Main conclusions

My thesis supports the following main conclusions regarding saproxylic beetles in south-central Swedish forestry and conservation:

- Conservation-oriented thinning has a substantial positive effect on oak beetles in oak-dominated forests for at least 10 years, and is therefore a useful management alternative over this time frame.
- At the local, per-stand level, spruce production forests (pre-commercially thinned, commercially thinned, not recently thinned) often support as many or more species of saproxylic beetles as do unmanaged stands (broadleaf- or spruce-dominated Woodland Key Habitats and spruce-dominated nature reserves), and their beetle fauna is worth more attention within forest management.
- Viewed at larger scales however, these production forests generally have a similar fauna from stand to stand, less diverse than that of Woodland Key Habitats. The latter therefore contribute to maintaining the biodiversity of saproxylic beetles in the region.
- Both at the local and landscape scale, the diversity and amount of broadleaf trees are associated with a higher diversity of saproxylic beetles. For saproxylic beetles, an increase of broadleaf trees in southern Sweden should be a priority in forestry and conservation management.
- The study of diversity patterns in forest ecosystems is complex, with interacting issues of scale-dependence, regional differences, and diverse, contrasting ecology of different species. The complexity requires more research, and should be highlighted in the debate around forestry and conservation.

In summary, my results agree with earlier authors pointing to the need for increased biodiversity considerations within Fennoscandian forestry, in addition to an increased number of protected or otherwise non-forestry areas (Niemelä 1997, Jonsson et al. 2005, Angelstam et al. 2020). Heterogeneity of habitats and substrates should be promoted by an increased use of mixed-species stands (Götmark et al. 2005, Gamfeldt et al. 2013, Felton et al. 2016), and an increased variety of management types (Brockerhoff et al. 2008, Götmark 2010, Felton et al. 2020). These changes would likely benefit not only saproxylic beetles, but the forest biota as a whole.

7 Acknowledgements

A very heartfelt thank you to my supervisor **Frank**, without whom I would not be doing research. Thank you also to examiners **Lotta** and **Bengt** and co-supervisors **Thomas** and **Alexandre** for help and input along the way.

I would like to thank **Peter Bergman** and Sveaskog for being helpful in providing map data and study sites, and the landowners who lent their forests to the Swedish Oak Project.

Thank you to **Niklas Franc** and **Thomas Appelqvist** for introducing me to the wonderful world of beetles. Thank you also to **Olof Persson** for being someone to share that interest with.

A big thank you to all my friends and colleagues at BioEnv throughout the years. A special thank you to my fellow PhD students and other early-career scientists for all the fun lunch-time discussions, game nights, book clubs, and more: **Agathe**, **Alexander**, **Badreddine**, **Charlotte**, **Christina**, **Daniel**, **Darragh**, **Giedrė**, **Ida**, **James**, **Jenna**, **Jonathan**, **Kirsikka**, **Leon**, **Leona**, **Lina**, **Magnus**, **Maria**, **Mårten**, **Nicklas**, **Nicolas**, **Niklas**, **Patricia**, **Per**, **Svante**, **Tobias**, **Wilhelm**, and anyone I've failed to mention.

Thank you **Laima** for sharing life with me for the last few years.

Finally, I would like to thank my family for being endlessly supportive, and especially dad **Bengt** and aunt **Heléne** for sparking my interest in nature from an early age.

Funding for my PhD has been provided by the foundations 'Stiftelsen Oscar och Lili Lamms Minne', 'Carl Tryggers Stiftelse för Vetenskaplig Forskning', 'Helge Ax:son Johnsons stiftelse', and 'Herbert och Karin Jacobssons Stiftelse'.

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