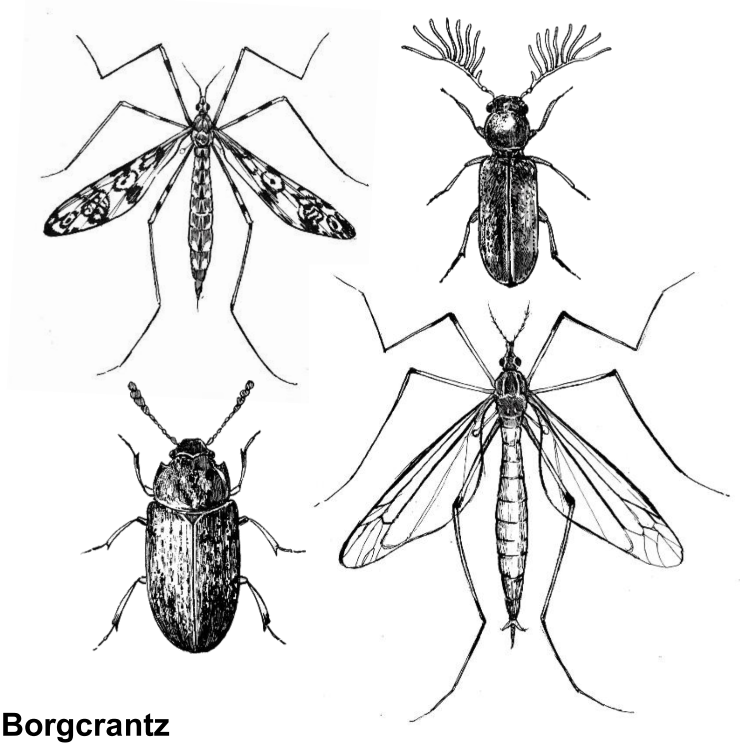
DEPARTMENT OF BIOLOGICAL AND
ENVIRONMENTAL SCIENCES

NEMORAL SAPROXYLIC INSECTS IN A CHANGING ENVIRONMENT

The effects of forestry on broadleaf saproxylic insects in Scania, southern Sweden



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Abstract

The negative effects of intense forestry on insect biodiversity has long been studied for the Scandinavian coniferous insects. Likewise, southern Sweden is undergoing a decline in old broadleaf forest when it is being logged or replaced with Norway spruce (*Picea abies*). About 70% of the Swedish red listed insects are found in the nemoral (broadleaf) zone, many of them being dead wood and broadleaf dependent, but still, recent studies are lacking on the effects of forestry from this area. As global temperatures rise, broadleaf trees such as beech (*Fagus sylvatica)* are expected to expand northward, which could create a biodiversity wasteland where intense forestry replaces beech with spruce plantation. Between April and August 2025, 40 pieces of dead wood gathered from pairs of beech and spruce stands were used to hatch saproxylic insects, comparing abundance in relation to stand, decay class and wood volume as well as species richness. In total, 167 individuals from 26 species emerged, 4 of these emerging from spruce, making the difference in counts large. Most abundant species in beech were deciduous, the most common being a red listed species of cranefly. The almost complete lack of individuals in spruce logs is a sign that many nemoral insects struggle to find suitable habitats in spruce plantations, regardless of decay class or volume. Although, species richness was positively affected by higher decay class in both stands. The properties of the stands are arguably different – one being a young plantation and the other a natural stand native to the area, but investigating the effects of local saproxylic biodiversity is urgent to understand the effects of intensified forestry, especially as many species connected to *F. sylvatica* are already threatened. I find sharp differences in the species abundance, where spruce plantations in the nemoral zone seem to lack suitable substrate for saproxylic insects.

Keywords: Forestry, Sweden, *Fagus sylvatica, Picea abies,* saproxylic insects, nemoral zone

Sammanfattning

De negativa effekterna av intensivt skogsbruk på biodiversiteten av skalbaggar har länge studerats, främst för insekter som lever i barrträd. I södra Sverige sker också en minskning i gammal ädellövskog när denna avverkas eller ersätts med rödgran (*Picea abies*). Ungefär 70% av Sveriges rödlistade insekter hittas i den nemorala (ädellövskogs-) zonen i Skåne, och en stor del av dem är vedlevande och beroende av ädellövträd, men trots detta saknas studier om skogsbrukets påverkan på dessa arter. Allteftersom att globala temperaturer stiger, förväntas utbredningen av bok (*Fagus sylvatica*) flyttas norrut, vilket kan komma att skapa en ödemark där ädellövträd till följd av skogsbruket ersätts med granplanteringar. Mellan april och augusti 2025 samlades 40 bitar död ved in från lokaler med bokskog och granplanteringar för att kläcka insekter och jämföra artantal i förhållande till trädbestånd, röta och volym samt för att mäta artdiversitet. Totalt kläcktes 167 individer från 26 olika arter, varav endast 4 individer kläcktes från gran, vilket gör skillnaden mellan bestånden stor. Majoriteten av de arter som kläcktes från bok var ädellövskogsrelaterade, där den vanligaste var en rödlistad harkranksart. Bristen på arter i granved är ett tecken på att arter i det här området har svårt att hitta levnadsmiljöer i granplanteringar, oberoende av vedens ruttningsstadie eller volym, dock syntes en positiv effekt av högre ruttningsstadie för artdiversiteten i båda bestånden. Beståndens egenskaper skiljer sig i grunden mycket, då ett av dem är en ung plantering och det andra en naturligt förekommande och fritt växande skog, men att undersöka effekterna av förändrad biotop på vedlevande biodiversitet är ändå viktigt för att förstå effekterna av ett intensifierat skogsbruk, särskilt när många arter kopplade till bok redan är hotade. Jag ser stor skillnad mellan mängden arter i bok och gran, där granplanteringar i den nemorala zonen tycks sakna passande substrat för nemorala vedlevande insekter att leva i.

1. Introduction

1.1. Background

1.1.1. The Swedish forestry model

Intense land use is causing several issues for the global biodiversity. Insects, contributing to one of the largest groups of biomasses on earth, have for the past decades suffered severe biodiversity loss due to intensified deforestation (John, et al. 2023) and agriculture (Outhwaite, et al. 2022). Restoring natural areas and protecting wildlife species has been a global goal for many countries to mitigate anthropogenic impact and improve biodiversity health. The UN has stated three goals under their *Agenda 2030* that directly address the protection of global biodiversity; goals 13, 14 and 15; goal 15 stating the promoting of sustainable use of terrestrial land and sustainably managing forests (United Nations, n.d.). Sweden, being a part of the UN since 1946, plays a large role in the combating deforestation act, with a new forest policy accepted in 1993 that states a higher level of responsibility for private forest owners in their forest management (Persson, 1996). In 1903, Sweden implemented the Swedish Forest Act, which states that previously forested land requires reforestation after timbering (Swedish Forest Industries, 2025). The harvested timber is meant to act as a CO_2 mitigator, as the wood stores the absorbed carbon dioxide, and becomes a sink when the lumber is used in carpentry or house building etc (Anon., 2025; Olsson & Johansson, 2025). The Swedish forest management is therefore meant to apply to the environmental goals of Agenda 2030, but as European Union suggests avoiding clearcut forestry to maintain a healthy forest environment (European Commission, 2023), the Swedish forestry model has been under criticization. The main method in Swedish forestry includes clear cutting deforestation and plantations being mainly monocultural, causing a lack of niches for specialist species, as well as fewer old-growth stands. Between 2003 – 2019, about 19% of the unprotected old growth forests in Sweden were logged (Ahlström, 2022), which affects many species negatively. Old growth stands are very important because they harbour many threatened species of invertebrates (Martikainen, et al. 2000; Brunet, 2004; Stenbacka, et al. 2010) and birds (Brunet, 2004; Rosenvald, at al. 2011); thus, these problems suggest that Sweden does not live up to the 15th goal. Sweden, being a forest dominated country with many species specifically dependent on trees, has thus met many issues in combining the intensely managed forestry with preserving national biodiversity. In 2020 there were 2453 species living in forests on the Swedish red list, which accounts for 52 % of the total amount of forest related species (SLU Artdatabanken, 2020). Of these species, 2041 (43 %) are primarily forest-dependent, making this group the largest out of the landscape types measured (SLU Artdatabanken, 2020).

1.1.2. The nemoral zone

Southern Sweden biologically differs a lot from the rest of the country, being a part of the nemoral zone (fig. 1). Blekinge, Halland, parts of Västergötland, Bohuslän and Scania (Swedish: Skåne) are a part of this geographical division, which is defined by its forest stands primarily consisting of deciduous woodland, making it a hot spot for Swedish red-listed species due to the rare biome (Mattiasson, 2004). The zone has a milder temperature than the rest of Sweden, where spring usually starts earlier and yearly temperatures generally being higher, which is closer related to the central-European climate. Skåne has during the past decades been undergoing a noticeable change in forest structure, mainly due to an intense change in forest management (Lindbladh, et al. 2014). In 2004, about 60 % of Sweden's red-listed species, and 70 % of the total amount of red-listed beetles (*Coleoptera*) were found in Skåne, which accounts for 2,5 % of the Swedish land area (Mattiasson, 2004). In 2020, 254 (27 %) were forest-related (SLU Artdatabanken, 2020).

Clearcut forestry has been dominating the Swedish forestry since the 1950's (Lundmark, 2020), and the nemoral zone has during this time seen a large reduction of broadleaf trees. During the 1960's, about 800 ha of the Swedish beech forests were logged a year, over 80% being replaced with spruce plantation (Brunet, 2004). The amount of spruce in southern Sweden increased with an estimated mean of 1000 ha a year between 1920-1985 (Falkengren-Grerup, 1995), and especially Skåne has seen a large decline in broadleaf forest, whereas the share of spruce in the total stand volume has increased (Holgén & Bostedt, 2004). In total, 77 % of the productive forest land in Götaland (southern Sweden) is owned privately (Skogsstyrelsen, 2023). Private productive forest accounts for 50 % of the Swedish forest land (Roberge, et al. 2020) and follows national jurisdiction. About 39 % of the productive forest land in Götaland consisted of spruce in 2021, the majority being about 40-50 years of age (SLU Riksskogstaxeringen, 2021). Most of the Scanian landscape has been heavily managed for centuries due to its fertile soil, but it is expected that the forests prior to the large-scale forestry implementation in the 1950's had a more heterogeneous composition (Lindbladh, et al. 2014). At the moment, many studies have been done on the effects of intense forestry on insect biodiversity above the nemoral zone where spruce grows naturally, but there is a knowledge gap for the south, meaning that not much is known about the effects on the nemoral biodiversity in recent years.

1.2. Saproxylic insects and Swedish forestry

Saproxylic insects are defined by their dependence on decaying wood during some part of their life cycle. They are often highly specialized on specific tree species, parts of trees, fungal rot, or stage of decay (species replace each other after time as the tree decays), making the group highly species rich, yet very vulnerable to change (Siitonen, 2001; Dahlberg & Stokland, 2004). Beetles make out a large group of saproxylic insects, 1260 species are found in Sweden, where 965 are fully dependent on deadwood (Dahberg & Stokland, 2004), Beetles also make out the largest group of red-listed saproxylic organisms (Dahberg & Stokland, 2004), as many species are being threatened by the intense forest management, mainly due to the lack of old-growth forests and dead wood (Müller & Bütler, 2010) and only a few number of species manage to attack living trees (Dahberg & Stokland, 2004). The amount of dead wood, correlating with the surface area of available substrate and thus the amount of space in which different species can specialize, here plays a huge role in the number of species occurring in an area. Likewise, the types of deadwood that is available (different stages of decay, species of tree and placement) have proven to matter in the question (Siitonen, 2001; Müller & Bütler, 2010). Intensely managed spruce plantations tend to lack this type of structure which many red listed species of saproxylic insects are dependent on, since the stands usually don't grow older than about 80 years before being clearcut (Hannerz, 2024). In managed spruce stands, about 6 % of the tree volume is dead wood, compared to natural stands, in which the stand volume of dead wood is around 10 – 40 % (Jonsson et al. 2016).

Many threatened species of saproxylic beetles lack a wide dispersal range, leading to a larger number being negatively affected by intense and large-scale forest management (Plath, et al. 2025). In spruce stands, dead wood (storm fellings, pest attacked trees etc.) also tend to be removed as not to increase the risk of the stands being attacked by the spruce bark beetle (*Ips typographus*) (Lindenmayer et al. 2008; Keskitalo, et al. 2016). The removal of this kind is commonly referred to as "salvage logging". Since many species of saproxylic beetles tend to either be conifer- or broadleaf specialists (Dahberg & Stokland, 2004), many species specialised on Norway spruce tend to be affected negatively where old-growth spruce forests are replaced by young plantations, as well as the broadleaf-dependent ones in the nemoral zone. More than 50 % of insects appear on broadleaf trees only, compared to about 25 % on conifers. Less than 10 % appear on both (Dahberg & Stokland, 2004). Beech, being a common species of tree in especially Skåne, hosts about 500 host specific red listed species, many of them saproxylic insects (Tingstad, et al. 2018), and the beech forests in this area make up for a large part of the areas where these species are abundant (Brunet, 2004). Overall, Sweden hosts many red listed conifer associated species seemingly due to the large volume of coniferous forest, although only a small portion of these are present in the nemoral zone (Tingstad, et al. 2018).

1.3. Factors affecting saproxylic insect species abundance

1.3.1. Stage of decay & dead wood accumulation heterogeneity

As saproxylic insects tend to be highly specialized, the species composition of a woodland site depends a lot on the variety of available dead wood. Dead wood can be accumulated in high volumes, e.g. after storms (Lindenmayer et al. 2008), but this also means that the dead wood is likely going to consist of the same or a rather homogenous quality, as the trees have died at the same time. Thus, continuous forests harbour a higher diversity in decay due to a continuous addition of available wood, and therefore a higher variety of saproxylic species. The dead wood availability here also depends on the productivity and decay rate of the site; the highest volumes are found in areas where the stand has high productivity, yet low decomposition rates (Seibold & Thorn, 2018). In managed forests, most of the large dead wood comes from human interference, such as forest thinning. In this case, the variety of dead wood also tends to decrease, as (I) the dead wood is created simultaneously, (II) the thinning is being done on younger trees, meaning that thicker dead wood from older trees is more uncommon and (III) the created dead wood is to a lesser extent sun-exposed due to the shading from standing trees in vicinity (Seibold & Thorn, 2018). In productive forests, on the other hand, trees are usually removed after thinning or salvage logging, leaving even less dead substrate for the saproxylic fauna (Lindenmayer, et al. 2008). A large number of threatened species tend to be positively affected by a higher stage of decay, while non-threatened species tend to be more present in lower stages of decay (Procházka & Schlaghamerský, 2019).

1.3.2. Wood volume

Combined with the distribution of available dead wood in an area, the volume of dead wood is in many cases positively correlated with species abundance, where a larger volume of the wood tends to host more threatened species, while non-threatened species seem to thrive in thinner dead wood (Procházka & Schlaghamerský, 2019). In beech, many threatened species of insects likewise seem to be abundant in lesser wood volumes coming from tree limbs (Scheigg, 2001), although shared a 82.6% overlap with tree trunks, meaning that a diversity in wood volume is necessary for a high species abundance, combined with dead wood continuity. Thus, wood volume and stage of decay combined matter for species abundance.

1.3.3. Stand age heterogeneity & species of tree

Due to the replacement of broadleaf trees with spruce, it is expected that many species connected to broadleaf wood are declining in numbers, as many red listed saproxylic species are found in old growth stands (Stenbacka, et al. 2010), where individual trees maintain old tree qualities such as lateral and vertical large dead wood and bark cavities. Sun-exposed, large dead wood is a seemingly important substrate for many saproxylic species (Seibold, et al. 2015). Many species also seem to be affected negatively by a denser canopy cover (Edelmann, et al. 2022; Plath, et al. 2025), which is a known effect in intensely managed spruce stands, where trees are often planted tightly, but this, according to Edelmann et al. did not seem to affect broadleaf dependent species as much. On the other hand, a higher number of conifers per stand seemed to affect most species of saproxylic species positively, except for the broadleaf specialists. A reason for this might be the specific ecological similarities and differences between beech and spruce – both being shade-tolerant, smooth-barked species of trees. Beech stands tend to harbour a less diverse abundance of ground flora due to the dense canopy cover and leaf litter, leading to a lower species diversity of insects but high numbers of specific ones. Thus, beech and spruce stands have similar qualities and have shown to be statistically indistinguishable in some ways (Plath, et al. 2025). This, mentioned in the study presented by Plath, is most likely connected to the amount of available dead wood – spruce plantations being highly infested with *I. typographus* create a larger species diversity than the beech stands, were dead wood tended to be absent due to removal. Specialists on broadleaf trees would on the other hand be expected to decrease with an increasing percentage of coniferous trees due to their niche. Likewise, the surrounding forest seems to play an important role in accumulating a higher diversity in saproxylic species in coniferous plantations in the hemi-boreal zone of Sweden, where spruce plantations surrounded by a majority of broadleaf forest affected the number of species positively (Gran, 2024). This would be expected to play an even more important role in the nemoral zone, where the landscape originally consisted of broadleaf trees only (Brunet, 2004; Lindbladh, et al. 2014).

1.3.4. Climate change

Increasing yearly temperatures due to climate change today play a big role in species distribution and local climate, where many central European species show up in southern Sweden more frequently due to the shift in climate zones. Many northern species are generally highly specialized due to the harsh environment which they are adapted to, making increased temperatures a large threat to them as well as other specialists (Neff, et al. 2022), leading to a poleward or latitudinal shift in species distribution to fulfil their niches (Klimaszewski, et al. 2021). The increased temperature is also expected to shift tree species distribution northwards, whereas broadleaf trees would be expected to move further north (Castillo, et al. 2022; Dyderski, et al. 2025). This shift, combined with the increased areas of managed spruce forests in southern Sweden, could possibly turn this area into a dead zone, where boreal species can't survive due to heat, and species moving further north from central Europe cannot survive due to their niches being underrepresented. Likewise, climate change and increasing global temperatures increases the amount and local impact of natural disturbances, such as storms and pest attacks (Patacca, et al. 2022), resulting in large-scale loss of lumber in areas dominated by silviculture, where dead wood is lost due to salvage logging. The outbreaks of insect attacks has been documented to increase in spruce dominated zones affected highly by drought during the summer, where *I. typographus,* due to warmer and longer summers, can manage to fulfil two reproductive cycles instead of one (Jönsson, 2007; Patacca, et al. 2022), as well as the drought affecting the spruce negatively due to its bad susceptance to heat (Keskitalo, et al. 2016).

1.4. Aim

Since many studies have been done on the species composition of saproxylic beetles in beech dominated forests in southern Sweden (Brunet & Isacsson, 2009a; 2009b; 2010), this study aims at studying the effects of forestry on saproxylic species in these areas, as most studies done on spruce plantations in southern Sweden are concentrated around Jönköping or Kronoberg in Småland or the boreal zones of northern Sweden (Stenbacka, et al. 2010; Jonsell, et al. 2019; Gran, 2024), where spruce is naturally common, and productive forestry has been implemented longer. For this study, 3 main questions are being asked about the species composition of saproxylic beetles:

- Does saproxylic insect diversity differ between beech and spruce in the nemoral zone?
- To what extent is species abundance correlated with deadwood properties, such as volume or stage of decay?
- Do the compared stands depend on deadwood properties for species abundance or is species abundance correlated to the stand?

The main hypotheses are that beech dependent species will be lacking in spruce plantations due to their specialization, and that spruce plantations instead will harbour generalist species, which might appear in both stand types, or nothing, making species abundance mostly dependent on stand rather than other aspects.

2. Materials and method

2.1. Study area

In this study, areas were chosen in Klippan, Örkelljunga and Ängelholm municipality of north-western Skåne (fig. 1); this being a part of Skåne mainly consisting of broadleaf or mixed stands, as it is connected to Hallandsåsen and Söderåsen which have a high forest cover unlike most of the Scanian plains where forest stands are usually small and fragmented due to agriculture and civilization. Söderåsen harbours the largest old growth stand of beech in Sweden (Brunet & Isacsson, 2010), consisting of trees that populated the area around 200-600 AD (Bergman, 2000). Large parts of the forest covered area of Skåne are today heavily managed, as the largest percentage of the land in southern Sweden is privately owned (Lodin & Brukas, 2021; Skogsstyrelsen, 2023). It is therefore usual for landowners to replace broadleaf stands with coniferous saplings after clearcutting, leading to a large-scale landscape change since the 1960's, where many spruce stands have reached ages of at least 60 years. This due to the implementation of silvicultural regeneration instead of natural, which was applied in the 1950's (Lindbladh, et al. 2014).

Each location was selected as a spruce plantation area in close vicinity to beech forest, with the assumption that the plantation itself had been planted on former beech land. The selection of areas was done by studying aerial photos from 1960 through the map function provided by Lantmäteriet, where locations with spruce plantations existing in photos from 1960 as well as current photographs were chosen in pairs with beech stands in the same area that had remained

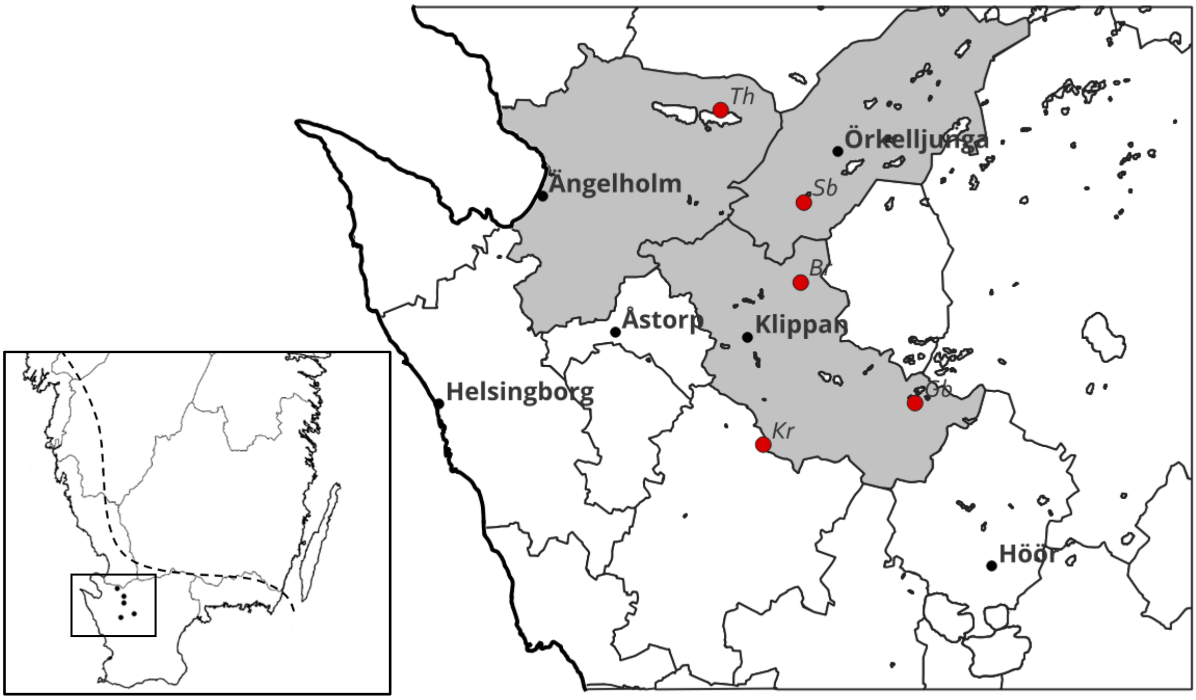


Figure 1: Map showing the chosen areas (red) and municipalities (grey). Site namnes are abbreviated, where Th = Trollehallar, Sb = Sjöbygget, Br = Bjärröd, Gb = Gustavsborg and Kr = Klåveröd. The line in the overview map represents the approximate divide between the hemi-boreal (above the line) and nemoral zone (below the line).

unharvested. Since the areas surrounding the spruce plantations consist of beech, the spruce plantations can be assumed to have been planted on former broadleaf forests. The aerial photos from 1960 were compared to current photos, and spruce plantations that were still standing were selected, as these stands should be old enough to harbour an arbitrary amount of dead wood, in comparison to younger stands. These will likewise have a higher number of species and thus make out a better comparison to the beech stands. Since the Swedish law of broadleaf forests (Ädellövskogslagen, now a part of the Swedish law of forestry, Skogsvårdslagen) was instituted in 1984, there were no regulations in 1960 considering replanting of broadleaf trees on harvested former broadleaf stands, meaning that planting spruce was legal by that time (The Swedish Parliament, n.d.).

2.2. Field work

From each stand, 4 pieces of lying wood was selected to be used for beetle hatching, making a total of 40 pieces. The branch sizes were selected through a diameter range between 5-30 cm, (preferably at 10 cm or larger since most species (red-listed and non-red-listed) are commonly found within that diameter range (Dahberg & Stokland, 2004)), and either picked or sawed off from larger logs. Wood objects could have been randomized, but this added the risk that the branch sizes would reach a standardized medium, instead of having all sizes represented. Most spruce stands were highly shaded, as the canopy cover in these kinds of plantations is tight. The same went for beech stands, but as the trees weren't growing as densely, some pieces of dead wood were sun exposed, but this was not accounted for in the study. The last piece of dead wood was collected on April 19th, and each wood object was placed in a closed, thick cardboard box with test tubes attached horizontally on the outside, labelled with location name, forest type (S/B) and log number (1-4) (e.g. Klåveröd B3). The boxes were left under roof until August 15th in practically outside temperature until insects had hatched.

The substrate was divided into decay classes according to the method used by Siitonen & Saaristo where the dead wood was scored from 1-6: (1) the wood is fresh, at most 1 year old, (2) the wood is fresh, but more than 1 year old, (3-6), the decay is measured through how far a knife can be pushed into the wood: (3) 0.5-2 cm, (4) 2-4 cm, (5) $\geq$ 5 cm, with the wood maintaining its original form and (6) $\geq$ 5 cm with the wood completely disintegrating (Siitonen & Saaristo, 2000).

2.3. Hatching & species identification

When the insects hatch, some of them are drawn to the light emitted from the transparent test vials and gather inside them to later be collected, as shown in previous studies using this method (Dahlberg, 2023). Boxes were checked every week and eventually emptied if any species hatched. Easily identifiable species were noted on the spot and released. Saproxylic species of *Diptera* were as well counted into the study, as they soon became the most abundant to emerge. At the end of the hatching process, each box was emptied onto a white sheet where insects that had not emerged into the vials (e.g. species that stay underneath the bark) were collected by hand. Saproxylic species were identified as saproxylic according to Artfakta and supervisorial help, and broadleaf or conifer dependent based on available information on SLU Artfakta, which was documented together with the location in which they were found as categories for each species as habitat and substrate preference, e.g. conifer dependent found in conifer forest. The preference was as well based on information found in Artfakta. Species that needed expert identification were sent to external supervisor. For exact identification of some individuals of *Ciidae,* genetalia preparation was used.

2.4. Data collecting

Table 1: Dead wood measurements used in model (*) and other measurements noted for the study.

Variable	Description
Stand type*	*Fagus sylvatica* or *Picea abies*
Branch diameter	Diameter of wood
Log volume*	Total volume of sampled log
Decay class*	Scale 1-6 based on method used by Siitonen & Saaristo, 2000
Habitat preference	Broadleaf forest, conifer forest, both

2.4.1. Species composition parameters

Each species was given a category based on given information in *Artdatabanken* and *Danmarks BilleBank* depending on which habitat type it normally prefers, divided into either deciduous, coniferous or both (generalist). Categories were used to determine whether either type appeared in the opposite type of stand. As too few species emerged from the spruce logs for a comparison to be drawn on species composition, species standing out were used in discussion instead.

Species diversity was measured for each stand and decay class 2-3 using Shannon Wiener diversity index. For the most sampled species, effect on emergence by stand, 3 stages of decay and volume were determined through a generalized linear model.

Figure 2a: Example of spruce dead wood in Trollehallar, Örkelljunga municipality and 2b: beech in close vicinity to a spruce plantation, Trollehallar.

2.4.2. Substrate parameters

Each site, located through historical and current aerial photos, was selected as a couple consisting of beech and spruce; the two stand types not being too far apart as to make sure comparisons between the two would not be affected by beetle dispersal range or fragmentation, but far apart enough to be counted as separate stands. The distance between the stands thus varies between 200 – 500 meters, making the total study site area about 43 hectares. The stands were divided into broadleaf or conifer depending on which tree type that dominated the stand. Spruce plantations and beech forest naturally tend to be dominated by either species due to the tree types being highly shade tolerant and dominant (fig 2).

The substrate decay class (see section 2.2.) was used to determine whether the decay had a significant impact on the species assemblage in each stand type. Dead wood has, as previously mentioned, a known positive impact on species diversity, where many red-listed species are drawn to dead wood of a higher decay class, whereas early successional dead wood usually contains a more homogenous species composition (Jonsell, et al. 2019). The stage of decay presenting the most variety of species were, according to Jonsell, et al. (2019) between 3-4, using the scale of Siitonen & Saaristo (2000). The substrate was therefore selected to have a similar range in decay between the stand types; the mean decay class being 3 for both stands. Wood diameter was documented and used to calculate an estimated volume using the formula:

$$V = \frac{\pi d^2 h}{4}$$

Where d = diameter and h = estimated length of the wood. The formula was divided by 2 again when the wood was not cylindrical and split in two. The volume was converted into litres.

As many factors play into the role of which species that harbour certain logs, (see 1.3) the factors considered during log sampling had to be reduced to not include e.g. log age or type of fungal rot, simplifying this to stage of decay. This generalizes the age of the log so that the stands can be compared, as spruce and beech harbour different properties when it comes to speed of the decay and which species of fungi that inhibit the wood.

2.5. Statistics

Statistical analysis was conducted in R version 4.5.1. As most individuals occurred once, the most sampled species (n ≥ 10) were selected for conducting model tests. Alpha diversity was calculated for all species.

2.5.1. Statistical tests & models

The 6 most sampled species never occurred in spruce, leading to predictors perfectly distinguishing the expected outcomes (complete separation). Therefore, a weak prior distribution was used to avoid extreme values (Gelman, et al. 2008). Visual diagnostics were used to ensure model fit and adherence to assumptions, based on the blme() function (Chung, et al. 2013) in the blme package as well as graphs in done ggplot() (Wickham, et al. 2019). For species counts, a generalized linear model was used from the lme4 package (Bates, et al. 2015), and for alpha diversity, Shannon Wiener diversity index and evenness were coded with the function(x) command (R Core Team, 2025).

2.5.2. Model parameters

The effects of stand, DC, site and volume was tested through a Bayesian linear mixed effects model (blme). As a generalized linear model would require added values to each stand and decay class to work, a blme works better with the number of zeros in the results. Data was beforehand crossed using Tidyverse crossing() function (Wickham, et al. 2019), creating a combination of each species and box (22x40). As DC1 and DC5 only appeared in one stand each, these samples created outliers for the model and were therefore removed – thus only 3 stages of decay were used in the blme. Only species with a count above 10 were tested, resulting in 6 models. Species counts were measured as binary (seen or not seen), due to individual counts risking overdispersion. For species counts, DC, mean volume and stand were used as fixed effects. No random effects from site were used due to the model not working, thus using a glm instead of a glme.

3. Results

In total, 167 individuals from 26 species emerged from the boxes – 20 of them appearing in beech only, 5 in spruce only and 1 in both (table 2). Not all species were included in the analytics, as some (i.e. *Phaeostigma notata* and *Strophosoma mellanogrammum*) do not really have a saproxylic stage, but rather use the tree in other ways, *P. notata* hibernating under the bark). Species that could not be fully identified (*Nemapogon sp.*) were also excluded. Out of

Table 2: Species found in the study as the total number of individuals (Tot) and occurrences overall and in both stand types.

Family	Species	Tot	Occurrence	Beech	Spruce
Coleoptera		**85**		**21**	**2**
Cerambycidae	*Alosterna tabaccicolor*	1	1		1
Cerambycidae	*Leptura quadrifiscata*	1	1	1	
Ciidae	*Cis boleti*	11	1	1	
Ciidae	*Cis castaneus*	1	1	1	
Curcolionidae	*Hylurgops palleatus*	1	1		1
Curcolionidae	*Rhyncolus ater*	3	2	2	
Curcolionidae	*Strophosoma melanogrammum***	1	1	1	
Dasytidae	*Dasytes caeruleus*	27	1	1	
Elateridae	*Denticollis linearis*	1	1	1	
Latridiidae	*Cartodere nodifer*	1	1	1	
Latridiidae	*Dienerella vincenti*	3	2	2	
Latridiidae	*Latridius minutus*	1	1	1	
Lucanidae	*Platycerus caraboides**	1	1	1	
Melandryidae	*Conopalpus testaceus**	2	1	1	
Melandryidae	*Orchesia undulata*	10	2	2	
Melandryidae	*Serropaplus barbatus*	1	1	1	
Ptinidae	*Hadrobregmus pertinax*	1	1	1	
Ptinidae	*Ptilinus pectinicornis**	16	1	1	
Pyrochroidae	*Schizotus pectinicornis*	2	2	2	
Staphylinidae	*Euplectus brunneus**	1	1	1	
Diptera		**73**		**11**	**2**
Tipulidae	*Tipula flavolineata**	37	6	6	
Limoniidae	*Epiphragma ocellare*	24	6	5	1
Asilidae	*Choerades marginatus*	1	1		1
Raphidioptera		**2**		**0**	**2**
Raphidiidae	*Phaeostigma notata***	2	2		2

Table 2, continued

Family	Species	Tot	Occurrence	Beech	Spruce
Leidioptera		**7**		**2**	**1**
Oecophoridae	*Oecophora bractella***	2	1		1
Tineidae	*Nemapogon sp.***	5	2	2	

**Mainly dependent on beech*
***These species were noted but not included in the study.*

Table 3: Summary of log measurements from beech and spruce. See appendix 3 for details.

Stand	Mean vol	Std. Deviation	Low	High	Mean DC
Beech	4.805	3.272	1.2	12.1	3
Spruce	4	3	0.8	15.6	2.75

the selected 26 species, 16 were counted as deciduous, 8 as generalist and 2 as coniferous. All species emerging in spruce stands were either coniferous or generalist – one of which mainly feeds on *P. abies* being the scolytid *Hylurgops palleatus*. *Serropalpus barbatus* was the only mainly coniferous species that hatched from a beech log. (Species preferences could not be added into models as categories are too subjective for numeral analyses but will be discussed later). Overall, the mean value of the species counts in the separate stands is highly different.

Table 4: Values for number of species per box and stand derived from generalized linear model. Significant values are bold.

Coefficients	Estimate	Std. Error	z value	p value
Intercept	0.054	0.416	0.131	0.896
Stand S	-2.157	0.531	-4.062	**<0.001**
DC 3	0.099	0.480	0.208	0.835
DC 4	1.334	0.447	2.982	**0.003**
Volume	0.007	0.046	0.153	0.878

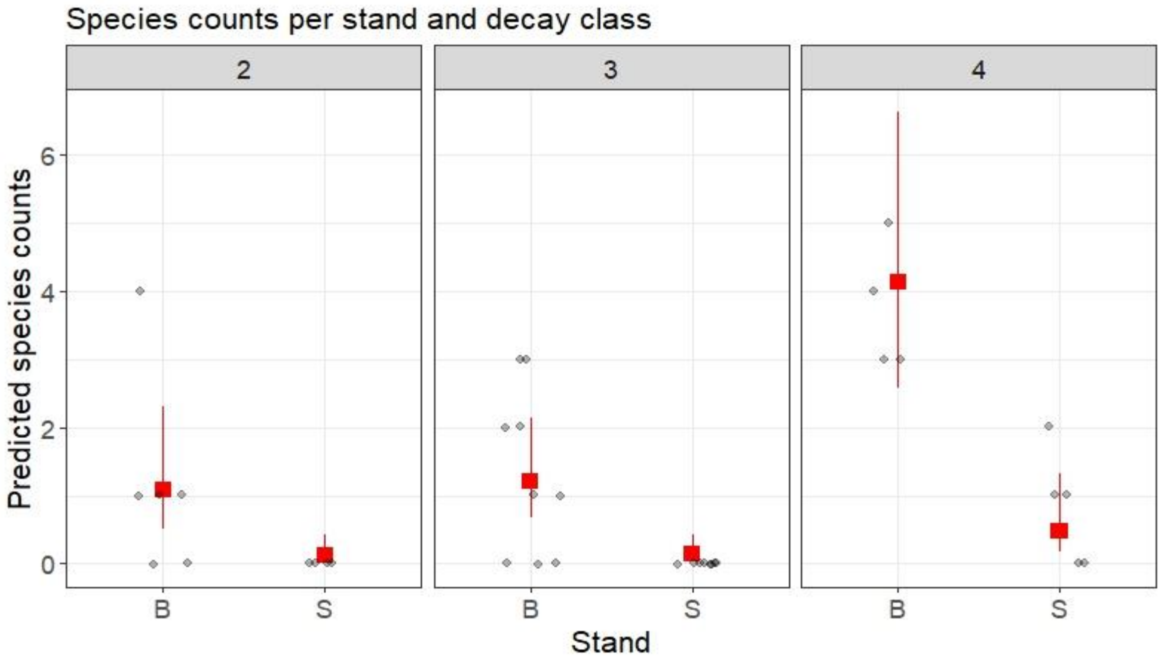


Figure 3: Species counts in each box for beech (B) and spruce (S) in decay class 2, 3 and 4 with expected species counts (red) and 95% CI derived from generalized linear model.

Notably for species counts, there is a significant difference between stands and for DC 4 according to the generalized linear model (table 3). The highest species abundance can be seen in DC 4 for both beech and spruce (fig. 3), but species abundance is overall low for spruce logs, resulting in a high significance for stand (table 4). Volume does not display any significance for species abundance.

Table 5a: Shannon diversity index and evenness for stand and DC

DC	Stand	Richness	Individuals	Shannon	Evenness
2	B	5	21	0.866	0.538
2	S	0	0	0	0
3	B	7	86	1.46	0.749
3	S	0	0	0	0
4	B	12	35	2.06	0.829
4	S	4	4	1.39	1

Table 5b: Shannon diversity index and evenness for stand, DC and sites with richness > 0. For sites with a species richness of 1, evenness cannot be calculated (-) and are thus not present in fig. 4b.

DC	Stand	Site	Richness	Individuals	Shannon	Evenness
2	B	Bjärröd	4	20	0.708	0.511
2	B	Gustavsborg	1	1	0	-
2	B	Trollehallar	1	1	0	-
3	B	Klåveröd	4	38	0.775	0.559
3	B	Sjöbygget	2	45	0.681	0.982
3	B	Trollehallar	2	2	0.693	1.0
4	B	Bjärröd	6	15	1.41	0.789
4	B	Gustavsborg	2	2	0.693	1.0
4	B	Klåveröd	1	1	0	-
4	B	Trollehallar	5	17	1.09	0.676
4	S	Bjärröd	1	1	0	-
4	S	Gustavsborg	3	3	1.10	1.0

Comparing alpha diversity in between decay classes using Shannon Wiener diversity index (fig 4a), species richness is higher in DC 4 for both stands, spruce displaying an evenness of 1, where one individual emerged from each species. For beech, diversity increases with decay class, although the number of emerging individuals is highest in DC 3 (table 5a), but over a lower species richness, as most individuals come from the same species – these mainly being the most abundant ones, *E. ocellare* and *T. flavolineata.* For this reason, evenness is very high in Sjöbygget (table 5b), as individuals are evenly distributed between two species. For DC 2, most individuals consist of *P. pectinicornis*, resulting in the lowest diversity index (fig 4a) and evenness (4b). The highest species richness was found in Bjärröd, DC 4, with a relatively high evenness, meaning that this site hosts a high number of species that are evenly distributed.

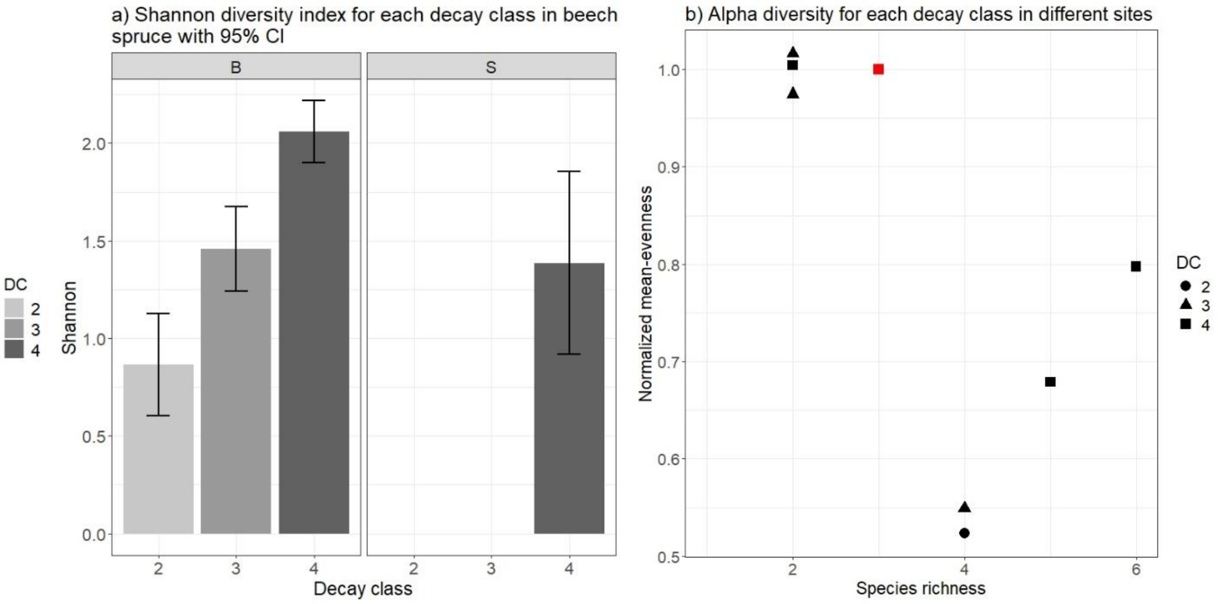


Figure 4a: Shannon Wiener diversity index derived from grouping species per decay class in both stands with 95% CI (spruce only has one bar as no species emerged in DC 2 and 3) and 4b: Species richness and evenness compared between specific sites. The dots represent sites with a species richness above 1 (table 5b) in each decay class. The spruce site is red.

Testing the effects for the most sampled species, no significance can be determined from either volume, DC or stand for all species but *T. flavolineata* (table 6f), which showed significance of stand. *E. ocellare* (table 6c) shows small evidence for association to stand, but no other association can be seen from the rest of the species.

Table 6a-f: Values derived from Bayesian linear mixed effects model for the most sampled species (n ≥ 10). Significant values (<0.05) are bold. Note that table 4a does not test the effects of decay class as this did not work with the model.

a) Cis boleti (n = 11)

Coefficients	**Estimate**	**Std. Error**	**z value**	**p value**
Intercept	-3.045	1.086	-2.804	0.005
Stand S	-1.578	1.661	-0.95	0.342
Volume	-1.09	1.225	-0.89	0.374
Random effect	**Variance**			
Site	0.561			

b) Dasytes caeruleus (n = 27)

Coefficients	**Estimate**	**Std. Error**	**z value**	**p value**
Intercept	-3.171	1.296	-2.447	0.014
Stand S	-1.514	1.683	-0.9	0.368
DC 3	0.468	1.434	0.326	0.744
DC 4	-0.879	1.930	-0.456	0.648
Volume	-1.212	1.220	-0.994	0.320
Random effect	**Variance**			
Site	0.661			

c) Epiphragma ocellare (n = 24)

Coefficients	**Estimate**	**Std. Error**	**z value**	**p value**
Intercept	-2.102	0.987	-2.130	0.033
Stand S	-1.805	1.033	-1.749	0.08
DC 3	0.847	1.111	0.762	0.446
DC 4	1.945	1.181	1.648	0.099
Volume	0.271	0.367	0.737	0.461
Random effect	**Variance**			
Site	0.332			

d) Orchesia undulata (n = 10)

Coefficients	**Estimate**	**Std. Error**	**z value**	**p value**
Intercept	-1.881	0.999	-1.884	0.059
Stand S	-1.986	1.571	-1.264	0.206
DC 3	-1.783	1.628	-1.095	0.274
DC 4	0.480	1.349	0.356	0.722
Volume	-0.460	0.796	-0.578	0.563
Random effect	**Variance**			
Site	0.604			

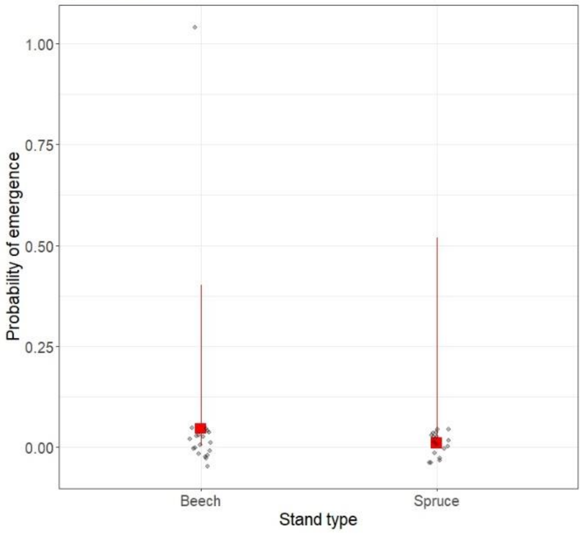
e) Ptilinus pectinicornis (n = 16)

Coefficients	**Estimate**	**Std. Error**	**z value**	**p value**
Intercept	-2.152	1.082	-1.989	0.047
Stand S	-1.457	1.704	-0.855	0.393
DC 3	-1.714	1.658	-1.034	0.301
DC 4	-1.347	1.760	-0.765	0.444
Volume	0.043	0.711	0.061	0.951
Random effect	**Variance**			
Site	0.632			

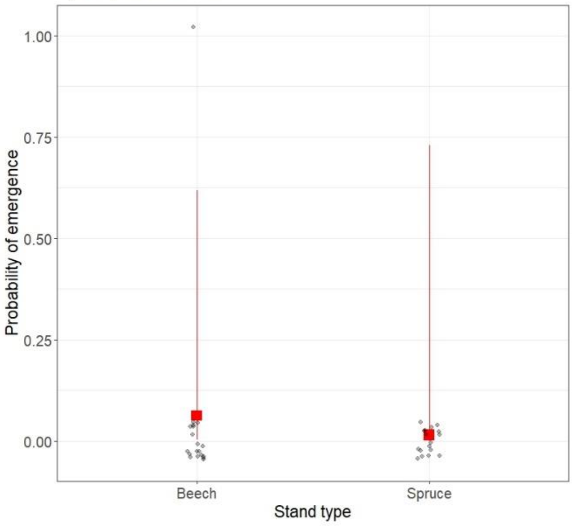
f) Tipula flavolineata (n = 37)

Coefficients	**Estimate**	**Std. Error**	**z value**	**p value**
Intercept	-1.443	0.981	-1.471	0.141
Stand S	-3.032	1.356	-2.236	**0.025**
DC 3	0.269	1.099	0.245	0.807
DC 4	0.745	1.229	0.606	0.544
Volume	0.342	0.471	0.726	0.468
Random effect	**Variance**			
Site	1.144			

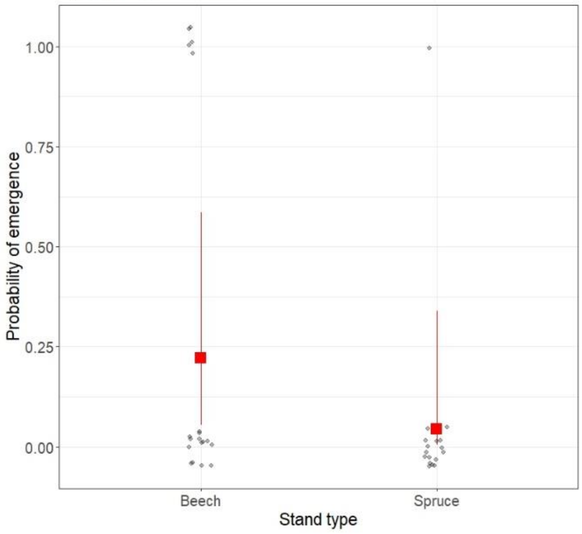
All the most sampled species show a higher probability of emergence (POE) in beech. *C. boleti* (fig. 5a), *D. caeruleus* (fig. 5b) and *P. pectinicornis* (fig. 5e) have a low POE overall, but



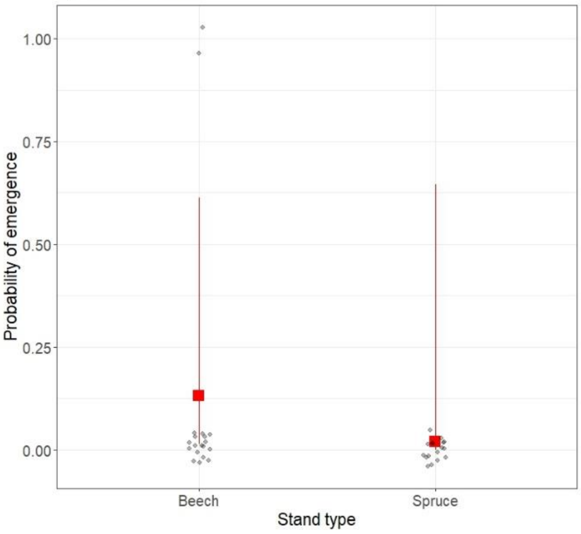
a) Cis boleti



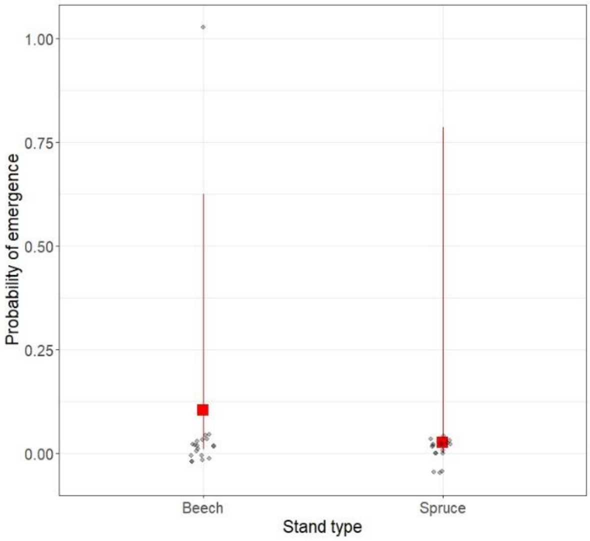
b) Dasytes caeruleus



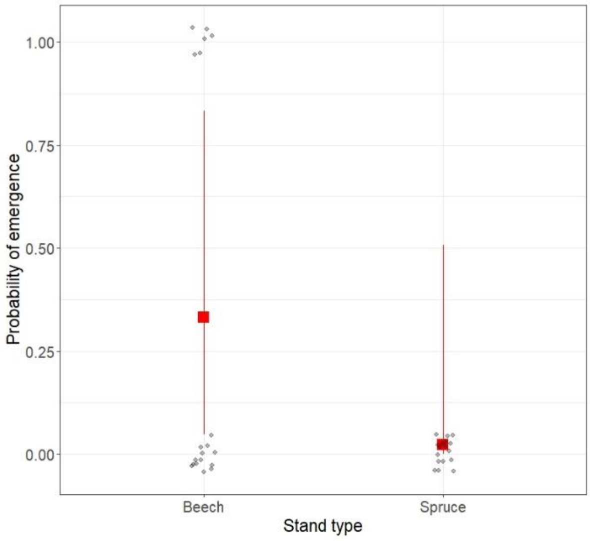
c) Epiphragma ocellare



d) Orchesia undulata



e) Ptilinus pectinicornis



f) Tipula flavolineata

Figure 5a-5f: Binary counts (emerged or not emerged) of the 6 most sampled species (n ≥ 10) in beech and spruce boxes. Probability of emergence is displayed with a 95% CI point range for stand type in the DC with the most accurate estimate (see table 4a-f). For C. boleti, DC is not included as a variable in the model.

this is expected, as these species only emerged in one box. Species emerging more frequently thus show a higher POE. In the figures, all boxes are displayed, while the point range only shows the probability from the most well-sampled decay class. For *T. flavolineata,* (fig. 5f) and *E. ocellare* (fig. 5c), this means that the POE is slightly higher, as they emerged from multiple decay classes (see appendix 3), and the single decay classes presented by the POE make up a part of the total number of logs. For beech, DC 2 = 6 logs, DC 3 = 9 logs and DC 4 = 4 logs. The decay classes presented per figure are a) 4, b) 2, c) 3, d) 2, e) 2 and f) 4 (see appendix 2 for details).

4. Discussion

There is a higher abundance in species richness in beech compared to spruce, despite decay class. Overall species abundance is positively affected by a higher decay class (fig. 3). None of the 6 species included in the Bayesian linear mixed effects model displayed a significant correlation with either DC or volume, although some of them might be positively affected by these factors in nature, e.g. *T. flavolineata*, which seemed to gain a higher estimated chance of emergence with an increased volume, although this displayed no significance when tested. Generally, a rather low percentage of a dead log is typically inhabited by saproxylic beetles, making it hard to draw conclusions about whether the low numbers were an effect of the study method or due to other external or environmental factors.

4.1. Species diversity increases with stand and decay class

The clear difference in species numbers between beech and spruce suggests a lower susceptibility to the properties of spruce plantations, especially as many species emerging in beech wood were deciduous. Between DC 2 and 3, no difference is visible when tested with the generalized linear model, although species diversity seems to be positively correlated with a higher decay class (fig. 4a), with a higher evenness of species in DC 4, where more species tend to be evenly distributed. For DC 3, a high number of individuals were present, although evenly distributed over a few number of species (table 5b), or in some cases unevenly distributed, leaving this decay class in between DC 4 and DC 2, where a large majority of the emerged population consisted of one species only. The most abundant species, *E. ocellare* and *T. flavolineata*, emerged in the largest numbers in DC 3, resulting in a low evenness where other species also emerged, in comparison to where the population only consisted of these two. The highest diversity index was found in DC 4, combined with a relatively high evenness in beech, and an evenness of 1 in spruce, where all individuals were of different species.

In the results, Shannon Wiener diversity index was not calculated in between stands only, but rather divided by decay class, as the difference in species richness in between stands is so clearly different. On the other hand, looking at decay class makes the stands more comparable. No species in spruce emerged from any other decay class than DC 4, and likewise in beech, we can see an increase in species diversity (fig. 4a), as well as evenness (table 5a) with decay class, meaning that the species in both beech and spruce in DC 4 are somewhat evenly distributed. Although the 4 individuals in spruce are hard to compare to the rest of the species emerging from beech logs, the complete lack of species in the other decay classes combined with the lower species diversity in lower decay classes for beech could indicate that species diversity is affected positively by a higher stage of decay, despite species of tree, at least for non-specialists. Both beech and spruce host many specialists (Dahberg & Stokland, 2004), and both broadleaf and conifer specialists tend to a high extent be positively associated with a higher amount of available dead wood (Müller, et al. 2010), suggesting that the plantations selected for this study lack the higher amounts required compared to the beech stands. Likewise, many rare species need dead wood of higher decay class (Jonsell, et al. 2019; Procházka, 2019), as well as dead wood created from older trees (Scheigg, 2001; Brunet, 2004). As the stand age differs a lot between the spruce and beech stands in this study, the higher species richness in beech is expected, yet a higher species richness in spruce plantations could be possible with higher stages of decay in the dead wood, despite the wood deriving from younger trees. Moreover, the number of species emerging from spruce logs in southern Sweden seem to be lower than in broadleaf trees but tend to increase when the dead wood is older, although tends to be less important for host-specific species (Jonsell, et al. 2007). This likewise seems to be the case here, where no host-specific species, but rather generalists, emerged from spruce logs.

4.2. Species abundance association to stand

Few species emerged from the spruce logs, also further emphasized by the values given by the generalized linear model (table 3). A clear difference is visible between the stands (fig. 3), especially in DC 4, suggesting that species abundance is strongly associated with stand. Spruce of higher decay class hosted, as mentioned, an evenly distributed number of species, although species abundance is very low compared to beech. On the other hand, the p-values for all species in the Bayesian linear mixed effects model except *T. flavolineata* are high for stand, even though spruce emergence is 0 for all of them. Due to overall low emergence, the estimated probability of emergence (POE) in the model for all the beetles (fig. 4a, b, d, e) is about the same for both stands except for the DC in which they emerged, although this does not necessarily imply that these species have the same probability of emerging from both stand types. Looking at the raw data (table 2), no shared species are present between stands except for *E. ocellare*, which, according to the model estimates, is more likely to emerge from beech than spruce. This would suggest that most species present in this study are more or less dependent on or more well-adjusted to one stand type.

4.3. Species abundance association to volume and decay class

None of the species tested in the Bayesian linear mixed effects model displayed any significant association to either decay class or volume, although species abundance overall was significantly higher in DC 4 (table 4), this decay class hosting the highest number of species for both stands. Volume had no significance whatsoever. Between DC 2 and 3, no difference is visible when tested with the generalized linear model, although species diversity seems to be positively correlated with a higher decay class (fig. 4a), with a higher evenness of species in DC 4, where more species tend to be evenly distributed. For DC 3, a high number of individuals were present, although evenly distributed over a few number of species (table 5b), or in some cases unevenly distributed, leaving this decay class in between DC 4 and DC 2, where a large majority of the emerged population consisted of one species only. The most abundant species, *E. ocellare* and *T. flavolineata*, emerged in the largest numbers in DC 3, resulting in a low evenness where other species also emerged, in comparison to where the population only consisted of these two. The highest diversity index was found in DC 4, combined with a relatively high evenness in beech, and an evenness of 1 in spruce, where all individuals were of different species. As all species emerging from spruce appeared in logs of this decay class (fig. 3), and this decay class also hosted the highest number of species (table 5a), species abundance could be expected to have a positive association to more rotted wood for both beech and spruce. This correlates with several previous studies done in both beech and spruce forests, where a higher species abundance is visible in higher decay classes (Jonsell, et al. 2019; Procházka, 2019), especially, threatened species are more abundant in even higher decay classes (5-6). As the highest decay class used in this study is 4, this correlates with a high abundance in non-threatened species, these being most abundant in DC 3-4 (Procházka, 2019). As DC 1 and 2 are given practically fresh wood, this means that most saproxylic species are positively associated with wood that has been decayed for some time, thus also being affected by polypores and other types of fungi, softening the wood.

The abundance of threatened species in beech seems, as mentioned in section 1.2., not to necessarily correlate with a higher volume, but rather tree age and parts of the tree (Scheigg, 2001). As many logs collected for this study were of lower volume, many species appeared in pieces of low diameter, and higher diameter and volume did not host more species than e.g. branches. The wood piece with the most species present had a diameter of 14 cm and a volume of 1.2 litres, thus being in the lower volume class (mean volume being 4.5 litres, see table 3), while another piece hosting 4 species had a volume of 4.4 litres (see appendix 2). Thus, no association between species abundance and higher or lower volume is present in the generalized linear model.

4.4. Discussing species

4.4.1. Species tested in blme model

Tipula flavolineata
The most sampled species was cranefly *T. falvolineata* (table 4f, figure 4f), which was the only species that displayed a statistical significance in the model, this being stand. The species is deciduous and specifically linked to white rotted beech, oak and elm dead wood. The species is listed as near threatened (NT) in Sweden (SLU Artdatabanken, 2020). It is abundant across Europe, but rare in Sweden, where most of the findings are done in the south. Threats likely include the lack of continuously available substrate as dead wood is removed and sites are fragmented, making it hard for the species to find suitable logs. Most encounters with the species during this study came from 2 sites: Trollehallar and Bjärröd (see appendix 2 for details) in higher decay classes. Although, *T. flavolineata* emerged from each DC, thus not showing a significance when tested statistically. As the logs from each site were collected from a restricted area, it is likely that smaller populations occur on these locations, where one or more females have laid multiple eggs in the available substrate. *T. flavolineta* had 6 occurrences in beech, meaning that the species emerged from 6 separate logs.

Epiphragma ocellare
The second most sampled species was cranefly *E. ocellare*, from which not much is known when it comes to the Swedish populations. It is recorded throughout most of Sweden, northwards along the coast, although most recordings are done in southern Sweden. It is abundant all throughout Europe where it inhabits woodland areas. In Denmark, larval development is recorded to mainly occur beech dead wood (Nielsen & Nielsen, 2009) (Byriel & Rojas, 2017), which would be expected to be the same in Scania, although there is a lack of sources on the species distribution and ecology in Sweden, where it is listed as not evaluated (NE). In this study, the species was abundant in beech (n = 23), occurring in 6 boxes over 3 sites. Most occurrences were together with *T. flavolineata,* where the two species rarely appeared separately. This could suggest that the two species depend on similar substrate. *E. ocellare* only emerged in DC 3 and 4, with a higher abundance in DC 4, and thus higher POE. The species emerged once in a spruce box, thus lowering the significance of stand in the model. As all emergences are counted as binary, a single observation weighs as heavy as multiple observations, increasing the POE in spruce despite this log lacking high abundance.

Orchesia undulata
Many beetles only occurred in one log but in high abundance. The only one that did not was O. undulata, occurring in 2 logs over 2 decay classes. The species itself is fairly abundant, as it

inhabits dead wood of various deciduous trees, mainly beech, birch and oak. The adult species inhabits polypores such as *Fomes fomentarius*, which is common on many deciduous trees, and rotting wood affected by fungi such as *Phlebia radiata,* common on many trees, and *Merulius tremellosus*, common on birch (Tamutis, Ferenca, & Pollock, 2019). In Sweden*, O. undulata* is listed as least concern (LC) and is recorded to be widely spread throughout Europe. In this study, the species was recorded from 2 logs, one of them in high abundance, likely hatched from one female. The highest abundance was recorded in DC 2, and one individual emerged in DC 4. Since the species mainly depends on fungi and fungi affected dead wood, DC or volume are likely not factors that contribute to species abundance, which is supported by the p values.

Ptilinus pectinicornis
Like the other beetles, *P. pectinicornis* only emerged in larger numbers (n = 16) from one log in total, likely due to one female having visited this certain log. It emerged together with 3 other species, one of them being *T. flavolineata.* The species is widespread in Europe, inhabiting multiple species of broadleaf trees, such as beech, alder and oak. The species inhabits any area with available host trees. No recordings are done on specific kinds of rot or presence of certain species of fungi, meaning that the species is most likely more bound to deciduous stands than any other factor. Here, as it only emerged on one occasion, the POE is overall low.

Dasytes caeruleus
Also emerging from one log in high abundance (n = 27), *D. caeruleus* emerged first out of all the species, hatching as early as April. According to SLU Artdatabanken, it mainly seems to inhabit deciduous trees but has been recorded in Norway spruce affected by *Fomitopsis serialis* in the hemi-boreal zone (Dahlberg, 2023). In southern Europe, it is recorded on decaying trunks of beech (Holtman, et al. 2014), although the species does not seem to be mainly beech depending on beech, meaning that the recordings in this study are likely correlated with the wood being of the right rot type, as the species in temperate areas usually inhabits white rotted deciduous trees.

Cis boleti
Lastly, *C. boleti* was recorded in one log (n = 10) of beech. The species is fungivorous, developing in polypore fruit bodies or fungi affected wood, typically white rotted. The main host polypores include *Trametes versicolor,* common on various deciduous trees, but favourably *Trametes gibbosa,* which preferably affects beech – the beetle being attracted to volatiles of *T. gibbosa* (Schigel, 2012). Like *O. undulata*, this suggests that the species abundance is not correlated with decay class or volume, but rather the right species of polypore, creating suitable kinds of rot. Here, *C. boleti* was recorded in DC 4, located in between tunnels and mycelia under the bark of the log. It was noted together with several other species, such as *O. undulata, Schizotus pectinicornis, Rhyncolus ater, Dienerella vincenti* and *Hadrobregmus pertinax. S. pectinicornis,* being mainly associated with damp broadleaf dead wood, and *O. undulata* and *D. vincenti,* being associated with fungi suggest that the log itself was likely affected by suitable polypores, thus resulting in many different species occurring, once again adding higher emphasis on fungal species rather than DC or volume. Due to the low emergence, this species also showed no significance in association to DC, volume or stand.

4.4.2. Coniferous species

Species emerging from beech consisted to a larger extent of deciduous specialists, with a smaller addition of generalist species. Three out of four species emerging from spruce were generalists: the polyphagous longhorn beetle *Alosterna tabaccilolor,* the robber fly *Choerades marginatus* and *E. ocellare*. Scolytid *Hylurgops palleatus* was the only mainly coniferous species to emerge from a spruce log. Only one notably coniferous species emerged from beech; *Serropalpus barbatus*, which normally inhabits spruce or pine wood. Notably, many species that specify on a certain species of tree do so in the early stages of decay as fresh wood differs more than rotted wood in between tree species – especially if inhabited by fungi. The "higher" the stage of decay, the easier it gets for the same kind of fungi to inhabit different species of wood. Beech and spruce naturally share some species in common due to their ecological similarities, meaning that it is not impossible for *S. barbatus* to regularly inhabit beech as well as spruce, although no sources can confirm this as for now. Most red listed saproxylic species are in some way connected to old growth forest, as these are decreasingly frequent and often confined to a small, fragmented area. *S. barbatus* seems to regularly inhabit *F. sylvatica* in warmer climates, such as in Italy (Parisi, et al. 2024) and Ukraine (Diedus, et al. 2022), opening the possibility that some species may widen their preferred substrate if needed. These individuals were on the other hand caught in suspended window traps, so there is no evidence that their larvae hatched from the wood itself.

Having deciduous species turn to coniferous trees is on the contrary not well documented. Norway spruce can be hard to inhabit when the wood is fresh due to resin which the tree uses do defend itself against pest outbreaks (Baier, et al. 2002; Zaman, et al. 2025), which is not the case for beech, making it possible for only a few species to be able to survive in living spruce trees, mainly scolytids, such as *I. typographus* and H. *palleatus*, which appeared in a spruce log in this study (table 2). Moreover, it might be harder for deciduous species to adapt to coniferous wood during the early stages of decay, and when old growth wood is lacking. Since beech takes longer to decay than spruce, especially as the overall productivity of warmer climate forests are higher (Seibold & Thorn, 2018), logs of the same decay class have likely been on the ground for longer, creating a longer spatial time frame for beetles to inhabit the wood, and creating a higher variety of niches meanwhile. This could also mean that the decay class does not correlate with the overall quality of the deadwood, as the same decay class in beech and spruce does not signify equal exposure to rot over the same amount of time, making the scale applicable for comparisons within the same or similar tree species, but not between coniferous and deciduous species, as conducted in this study. On the other hand, this indicates that spruce deadwood in the nemoral zone would be of lower quality as decomposition rates increase in a warmer climate. Wood-inhabiting fungi tend to serve as key drivers in decomposition (Goßmann, et al. 2025a), and many saproxylic fungivorous beetles here serve a role as vectors for spreading fungi between logs (Goßmann, et al. 2025b). If the abundance of saproxylic beetles decreases in young plantations, this might affect the amount of fungi inhabiting the deadwood, further decreasing the variety of rot present in an area.

4.5. Fragmentation and dead wood diversity

Species composition lessens with isolation and depends on dispersal of different taxa. Spatial distribution, according to Scheigg (2000) is a key mitigator for species richness; clustered areas of dead wood dispersed far away from other logs hosting lesser species than plots with high dead wood connectivity (Schiegg, 2000). As Skåne is a highly exploited area, many woodland areas are commonly fragmented, divided by urbanised areas, cropland, forest plantations or clearcut areas. This could affect the dispersal of small saproxylic species, making the areas in which they emerge extremely local, and in some cases too small for the species to thrive due to a lack of consistency in new suitable substrate. This has been the case for the red-listed click beetle *Denticollis rubens*, known from the Söderåsen-area (SLU Artdatabanken, 2020). Likewise, stage of decay seems to play a larger role for rare species when the trees are old, which once again emphasizes the age of the trees rather than a higher decay class, as many rare species lack suitable areas where many trees grow old enough (Brunet & Isacsson, 2009a). Areas that harbour a diverse dead wood composition with different stages of decay (where trees and branches die and rot continuously) would in this case be most suitable for a higher species diversity. This would suggest that the areas selected for this study lack a suitable dead wood diversity regardless of stand type, as no red listed beetles emerged from either, the only red listed species being *Tipula flavolineata*. Many red-listed species of saproxylic beetles also tend to lack a wide dispersal range and are therefore negatively affected by fragmentation (Brunet & Isacsson, 2009b). As the sites in this study consisted of beech and spruce stands in close vicinity, most areas of beech forest were small and fragmented by spruce plantations and clearcuts, possibly affecting the suitable habitats and habitat heterogeneity necessary for red-listed species to emerge.

Species composition is affected by numerous factors, as previously discussed. Many highly specialized saproxylic insects (often tending to be the case for old-growth dependent deciduous species) seem to need a continuous accumulation and dispersal of dead wood emerging from old trees; something that tends to be excessively rare as there is a lacking continuity in tree growth when the forest is heavily managed. Likewise, the possibility of old growth trees occurring within dispersal range when patches of forest are located too far apart lessens with increased fragmentation (Brunet & Isacsson, 2009b). Since this study only consisted of 5 locations, no conclusions can be drawn from the potential impact of the surrounding stands, but this might be a contributing factor in species composition and population dispersal, especially as many forests in Skåne suffer from severe fragmentation.

4.6. Deciduous and coniferous species in a shifting climate

As many studies suggest that climate change will create a northward shift of *F. sylvatica* due to its susceptance to increased temperatures, along with its competitiveness compared to *P. abies* (Coulson & Stephen, 2008; Bolte, et al. 2009; Falk & Hempelmann, 2013; Dyderski, et al. 2025). This shift would make it hard for coniferous species to adapt to the areas of spruce planted further southward, both due to the increased temperatures, but also due to the lower habitat quality as the plantations are evenly aged and therefor do not create enough deadwood and decay class diversity. This would mean that the nemoral zone is to be expanded further north in the future, meanwhile suitable areas for Norway spruce would shift even further northwards, as to a point where the southernmost parts of Sweden would no longer be suitable (Coulson & Stephen, 2008). Likewise, it would be expected that species distribution follows this same shift, where deciduous species follow the distribution of *F. sylvatica.* The communities of saproxylic beetles varies depending on climate regions, where southern species in warmer areas tend to be positively affected by shade, meanwhile they in northern regions prefer sun exposed areas (Goßmann, et al. 2024). Northern species seem to be positively affected by shade regardless, further emphasising that the geographical distribution of northern coniferous species would be expected to decline as temperatures rise. The findings of this study would suggest that coniferous species do not extend southwards as spruce is being planted in the nemoral zone, but rather that these plantations would be inhabited by already abundant generalists or nothing at all. To improve forest health, while maintaining biodiversity and lessen the negative effects of climate change on forestry, many studies suggest that forestry needs to shift from monocultural stands to mixed stands (Felton, et al. 2010; Edelmann, et al. 2022; Gran, 2024), while also lessening the effects of storm fellings (Bolte, et al. 2009).

Even though spruce is one of the species of tree that harbours the most associated saproxylic species (Stokland et al. 2012), this study would suggest that such species might not thrive in silvicultural plantations in the nemoral zone. In in my study conducted in 2023, many species related to spruce were found in vicinity to dead wood in spruce plantations, especially in areas affected by *I. typographus* (Borgcrantz, 2023)*,* but none of these were present during this study. As the previous study area was located in the hemi-boreal zone, it would be expected that more species adapted to coniferous trees would be abundant. As species were lacking in the coniferous stands, not much can be said about whether this applies for all spruce stands in Skåne. It could be expected that boreal species do not migrate southwards to inhabit these areas, as a northward and lateral shift in species distribution has been a trend worldwide (Klimaszewski, et al. 2021). Surrounding areas of broadleaf forest have proven to be beneficial for saproxylic biodiversity in the hemi-boreal zone (Gran, 2024), but whether this applies for the nemoral zone as well is unclear.

4.7. Limitations & further studies

Overall, trying to summarize the effects of large-scale forestry on an entire group of insects based on 5 locations is challenging, but hopefully the results in this study are sufficient for contributing to inspire further research about the subject. There are a few other limitations in the study design that can be improved, mainly the testing of effects from decay class. Firstly, only DC 2, 3, and 4 were sampled to a large enough extent that they could be used in the model, making it impossible to assess the importance of the full range of decay class. Secondly, POE in certain decay classes differ a lot due to the number of logs collected. For *E. ocellare* in DC 4, POE is about 50%, since only 4 logs were collected from this decay class and the species emerged from 2 of them (see appendix 3). Thus, displaying the overall POE was difficult as the probability increases with decay classes of fewer logs. Collecting the same number of logs from each decay class could solve this issue. Lastly, the amount of material was highly limited. As the study only was conducted by one person in a limited area during the span of roughly a year, more data is needed to draw any conclusions on species distribution and biodiversity overall, as a big limitation was the low number of species emerging. Due to the low chance of species hatching from a specific log, collecting logs might not be optimal. This was done as not to accidentally encounter species passing by through window trapping, but to further control the effects of the site on species accumulation, a better option would be to manually place logs on site and study the emerging species from said logs over a span of years, as the log gradually decays, and place traps onto logs on site. Each spring, the decay class of each log would be measured (to gather an understanding of the breakdown process and local productivity effect on the species of tree) along with a documentation of eventual species of fungi. This would eliminate the risk of accidentally collecting “empty” pieces of wood and more effectively seeing what species actively inhabit the logs over time.

5. Conclusions

Despite low species emergence, it is quite clear that insect species abundance depends on the stand and species of trees from which the dead wood is created. Decay class and volume showed no significance for the most abundant species, but a higher decay class had a higher species richness overall in both beech and spruce. Nevertheless, very few species in the nemoral zone seem to thrive in spruce plantations altogether. The few species that did emerge from spruce logs were mostly generalists, implying that some species might emerge from spruce stands by chance, but in low abundance. The most abundant species were mostly correlated with specifically beech or deciduous forest, thus telling us that there likely is a low abundance in species able to survive in coniferous stands. Species abundance in the nemoral zone thus mostly seems to rely on stand and species of tree, further emphasizing the fact that nemoral biodiversity might be at risk as the native stands are replaced under large scale forestry.

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Appendix 1: Popular science summary

The nemoral zone is declining, and it might harm a big part of the Swedish insect biodiversity

Sweden is known for its enormous seas of spruce and pine forests. Mixed in between, we have the broadleaf trees, although often looked over in the aspects of forestry. In southernmost of Sweden, on the other hand, the broadleaf forests dominate – or at least – used to. Although, no concerns seem to be raised, even though countless studies have been done on the negative effects of intense forestry on insects in natural spruce forests. How do species from an entirely different forest type react to this rapid change? In this study, logs from native beech forest were compared to logs collected from spruce plantations in Scania, southern Sweden to determine how the number of insects is affected by large-scale forestry when conducted in the broadleaf dominated area.

Southern Sweden harbours many species

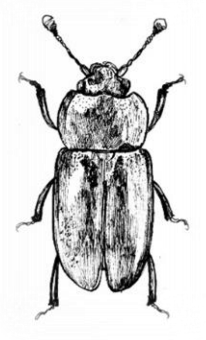
Southern Sweden biologically differs a lot from the rest of the country, being a part of the nemoral zone. Blekinge, Halland, parts of Västergötland, Bohuslän and Scania (Swedish: Skåne) are a part of this geographical division, which is defined by its forest stands primarily consisting of deciduous woodland, making it a hot spot for rare species due to the rare biome. The zone has a milder temperature than the rest of Sweden, where spring usually starts earlier and yearly temperatures generally being higher, which is closer related to the central-European climate. Intense forestry has been ongoing since the 1950's, and the nemoral zone has seen a large reduction of broadleaf trees since the 1960's, where the number of beech-dominated stands were reduced by 25 %, while the amount of spruce has been increasing with an estimated mean of 1000 ha a year.

Intense forestry harms many insects

Many insects depend on decaying deadwood. They are often highly specialized on specific tree species, parts of trees, fungal rot, or stage of decay, making the group highly species rich, yet very vulnerable to change. Intense forest management has reduced old-growth forests and dead wood, leading to fewer insects surviving in the Swedish forests. Intensely managed spruce plantations usually don't grow older than about 80 years before being clearcut, meaning that species depending on older trees have less suitable habitats. In these stands, about 6 % of the tree volume is dead wood, compared to natural stands, in which the volume of dead wood is around 10 – 40 %.

Beetles – a diverse group of insects

There are about 4500 species of beetles in Sweden, where 965 are fully dependent on dead wood. Beetles also make out the largest group of Swedish red-listed dead wood dependent organisms. In 2004, about 70 % of the total amount of red-listed beetles were found in Scania, which accounts for 2,5 % of the Swedish land area.



Southern Sweden lacks studies about intense forestry

Many studies have been done on the species composition of insects in beech dominated forests in southern Sweden, but most studies done on spruce plantations are concentrated around areas where spruce is naturally common and productive forestry has been implemented longer. Therefore, this study aimed at looking into the effects on biodiversity where spruce is not naturally common.

A beech forest in Scania fragmented by a spruce plantation

Do species thrive in a changed landscape?

The results tell us little about the species composition, but out of 26 species, only 5 emerged from spruce. No beech-related species appeared in spruce, and in beech, the majority were broadleaf dependent. None of the most occurring species appeared in spruce. This shows us that very few species in the Scanian area seem to thrive in the productive forestry landscape – something that might indicate a great biodiversity loss if the broadleaf forests keep declining.

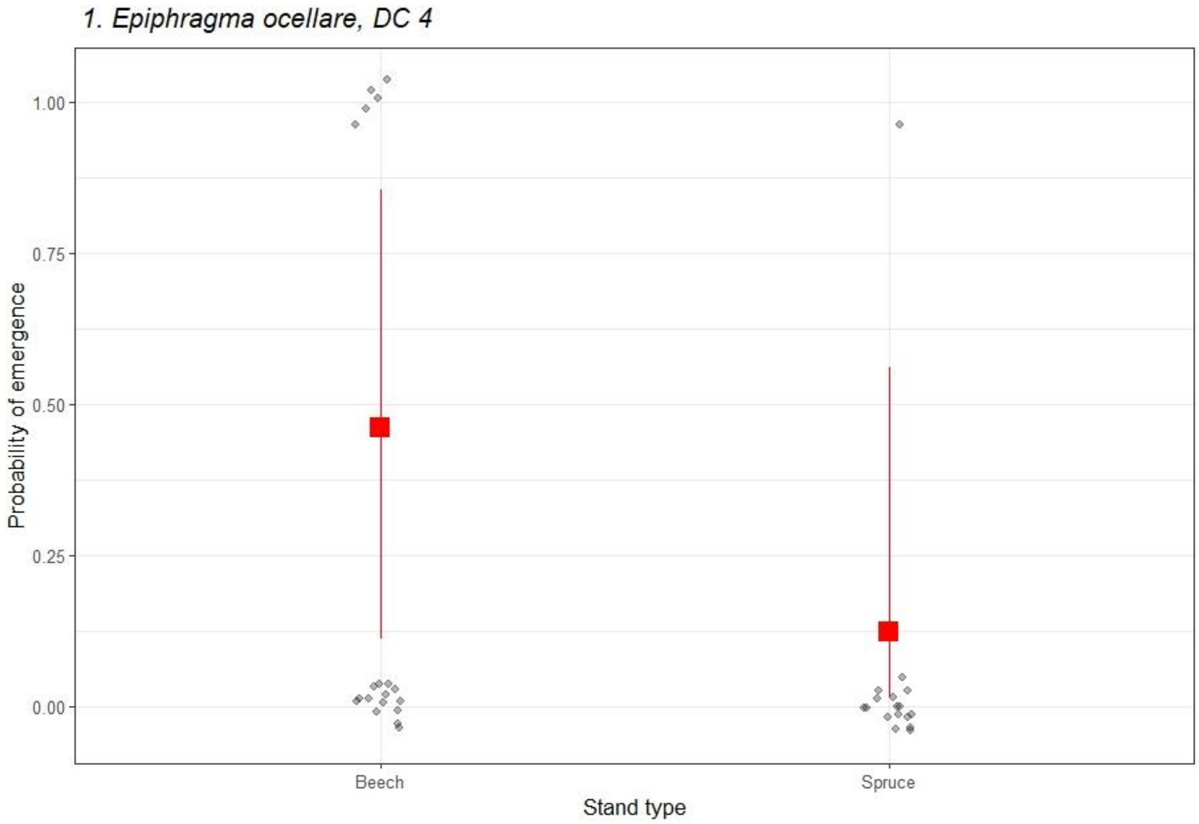
Appendix 2

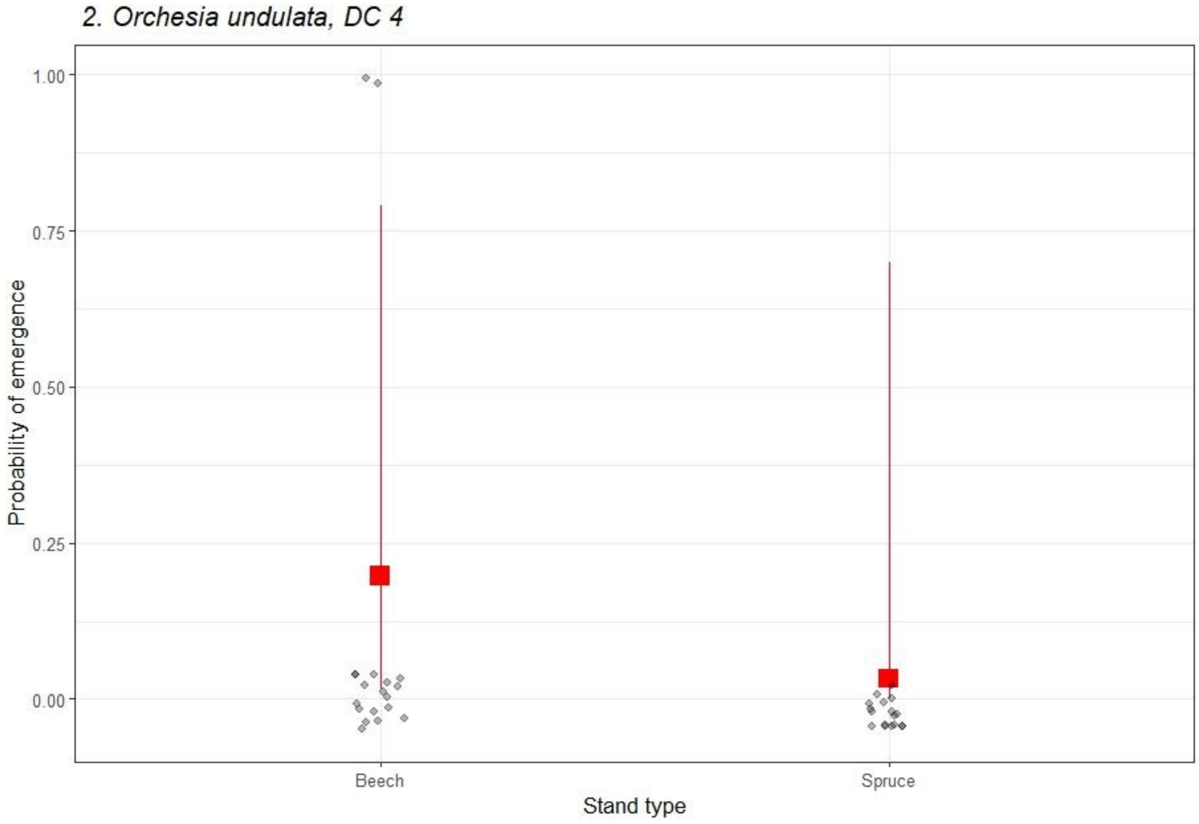
Table A1: Site and dead wood qualities. S stands for spruce, B stands for beech. DC = decay class

Site	Stand	No.	DC	Diameter	Vol (l)		
Klåveröd	S	1	2	22	2,4		
Klåveröd	S	2	1	7	5,2		
Klåveröd	S	3	2	21	15,6		
Klåveröd	S	4	1	5	1,7	tot vol	24,9
Klåveröd	B	1	2	7	4,6		
Klåveröd	B	2	3	18	8,4		
Klåveröd	B	3	5	15	9,8		
Klåveröd	B	4	3	5	1,2	tot vol	24
Trollehallar	S	1	3	23	7,9		
Trollehallar	S	2	3	11	2,6		
Trollehallar	S	3	1	6	1,3		
Trollehallar	S	4	3	8	1,6	tot vol	13,4
Trollehallar	B	1	2	18	3,1		
Trollehallar	B	2	3	10	11,1		
Trollehallar	B	3	2	5	3		
Trollehallar	B	4	4	12	1,4	tot vol	18,6
Sjöbygget	S	1	4	16	3,2		
Sjöbygget	S	2	3	16	6,4		
Sjöbygget	S	3	2	10	1,5		
Sjöbygget	S	4	3	21	6,9	tot vol	18
Sjöbygget	B	1	3	10	2,4		
Sjöbygget	B	2	3	9	5,6		
Sjöbygget	B	3	3	7	2,6		
Sjöbygget	B	4	2	7	1,3	tot vol	11,9
Gustavsborg	S	1	4	12	5,3		
Gustavsborg	S	2	3	25	4,3		
Gustavsborg	S	3	4	15	5,4		
Gustavsborg	S	4	4	10	2,6	tot vol	17,6
Gustavsborg	B	1	3	16	8,7		
Gustavsborg	B	2	4	28	12,1		
Gustavsborg	B	3	3	6,5	1,2		
Gustavsborg	B	4	2	16	4,4	tot vol	26,4
Bjärröd	S	1	3	11	3,8		
Bjärröd	S	2	3	16	4,4		
Bjärröd	S	3	4	5	0,8		
Bjärröd	S	4	2	9	2	tot vol	11
Bjärröd	B	1	3	14	4,2		
Bjärröd	B	2	4	11	3,3		
Bjärröd	B	3	4	10	3,3		
Bjärröd	B	4	2	14	4,4	tot vol	15,2
Mean B			**3**	**11,925**	**4,805**	**tot B vol**	**96,1**
Mean S			**3**	**13,45**	**4,245**	**tot S vol**	**84,9**

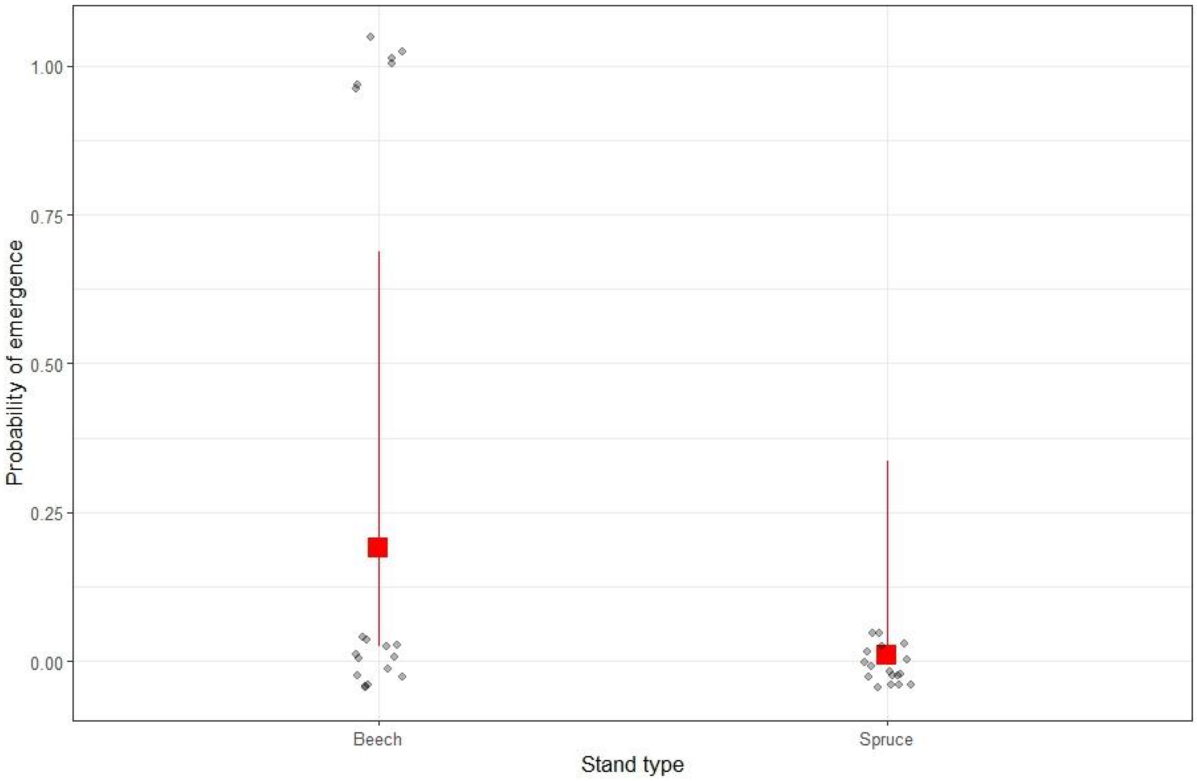
Appendix 3

Figure A1- A4 Species probability emergence in the other decay classes in which they emerged. Note that the emerged dots display every box. For E. ocellare, DC 4 is 2 emergences on 4 logs, O. undulata DC 4 is 1 emergence on 4 logs and T. flavolineata DC 2 is 1 emergence on 6 logs, DC 3 is 3 emergences on 9 logs.





3. *Tipula flavolineata, DC 2*



4. *Tipula flavolineata, DC 3*