Population dynamics of the spruce bark beetle *Ips typographus* in forest conservation areas and the interaction with biodiversity and natural enemies

Evelina Andersson

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Populationsdynamik hos granbarkborren Ips typographus i skogliga naturvårdsområden och samspelet med biologisk mångfald och naturliga fiender

Evelina Andersson

Supervisor:	**Simon Kärvemo, Swedish University of Agricultural Sciences, Department of Ecology**
Examiner:	Erik Öckinger, Swedish University of Agricultural Sciences, Department of Ecology

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Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Ecology
Unit of Forest Entomology

Abstract

Biodiversity is rapidly decreasing and in need of more conservation efforts. However, the tree-killing European spruce bark beetle, *Ips typographus* (L.), has made forest conservation controversial by affecting conservation areas and possibly adjoining managed forests, yet is still a keystone species leaving decaying wood promoting biodiversity. To improve our understanding of the influence of conservation areas, this study investigated the difference in population dynamics of the spruce bark beetle, abundance of natural enemies and species richness of arthropods, including their association to one another and differences in the environment, compared between managed forests, woodland key-habitats and nature reserves during an outbreak in southern Sweden. Bark samples were collected from standing trees in the different managements, and in each bark sample all arthropod species and information of the spruce bark beetle's population dynamics were recorded. Additionally, environmental data of local and regional landscape was obtained though remote sensing. The results showed that the conservation areas included in this study had e.g., higher spruce volumes and drier ground compared to managed forests and consequently had an environment theoretically more prone to attacks. Despite this, in particular nature reserves, did not have higher attack density, offspring production or reproductive success of spruce bark beetles, compared to managed forests. Under similar population pressure, even lower rates than managed forests. Furthermore, nature reserves possessed higher species richness per m^2 bark compared to managed forests, and generally higher abundance of natural enemies per m^2 bark compared to the other two managements. This suggests that nature reserves are able to allow natural ecological processes and maintain vital ecosystem functioning among spruce bark beetles and their natural enemies, resulting in high biodiversity and a natural control with possibly relatively high spruce bark beetle mortality. However, the influence of woodland key-habitats is more unclear and remains to be addressed.

Keywords: spruce bark beetle, population dynamics, conservation areas, biodiversity, natural enemies, species richness, managed forests, woodland key-habitats, nature reserves

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1. Introduction

The world's biodiversity is rapidly decreasing and is facing an ongoing mass extinction (Kolbert 2014; WWF 2022). To hold back the loss of important species, habitats and ecosystem functioning, conservation efforts are required to a wider extent (Raven & Wagner 2021; WWF 2022). However, during outbreaks of the tree-killing European spruce bark beetle, *Ips typographus* L. (Coleoptera: Curculionidae: Scolytinae), entire conservation areas can get damaged and thereby fail in its purpose of protecting nature (Schroeder & Weslien 2020). Consequently, conservation areas have often been accused of acting as sources of spruce bark beetles and increase infestations in the surroundings, and by that made forest conservation into a controversial question (Valeria et al. 2016; Wermelinger 2004).

1.1 Today's biodiversity conservation

In 2022, the UN Biodiversity Conference (COP-15) came to an agreement on increased national and international funding for biological diversity (Regeringskansliet 2022). They stated, by the year of 2030 the world's total area, of both land and sea, shall be 30% protected, and that 30% of all damaged ecosystems must be restored (Regeringskansliet 2022). Sweden has signed the Convention on Biological Diversity (CBD), and is obligated to this agreement (Naturvårdsverket 2023a). Moreover, two of Sweden's own environmental objectives include living prosperous forests, and a rich plant and animal life (Sveriges miljömål 2023b; Sveriges miljömål 2023a). At the moment, approximately 15% of Sweden's total area is conserved, about 9% of the total forest land is conserved, and near 6% of the productive forest land is conserved in Sweden (Naturvårdsverket 2021).

1.2 The European spruce bark beetle

Sweden consists of 68% forest land and consequently and made timber production an important renewable natural resource in the country (Sandström et al. 2011; SCB 2023). Additionally, Sweden's large amount of forest land provides great opportunities to establish forest conservation areas. However, in a changing climate and even-aged spruce forests, tree-killing pests have increased sometimes resulting in large-scale outbreaks causing forest loss making both commercial forests and conservation areas suffer (Schroeder & Weslien 2020; Wu & Nilsson 2023; Öhrn 2012). The host-tree species of the European spruce bark beetle is the Norway spruce, *Picea abies*, and the beetle usually attacks trees under the circumstances of forest disturbances, such as storms or droughts which cause stress and a reduction in the spruce trees' natural defence. However, healthy spruce trees can also get infested during epidemic circumstances, when enough beetles simultaneously invade a tree successfully and thereby exceeding the attack threshold which overcome the trees' natural defence (Mulock & Christiansen 1986). Furthermore, higher attack densities of the spruce bark beetle have shown to reduce their reproductive success, caused by limited breeding space and food resources, so-called intraspecific competition (Anderbrant et al. 1985; Komonen et al. 2011; Zhang et al. 1992).

To inhibit infestations of the spruce bark beetle, commercial forests are managed and have active pest-control, like thinning, trap trees, insecticides, and debarking (Grodzki et al. 2006; Mergl et al. 2021), and logging being a common method in Sweden (Lindelöw & Schroeder 2008). Conservation areas, on the other hand, have no active pest-control, and are usually left untouched (Naturvårdsverket 2023c). Because of this, conservation areas have in some cases shown to be more prone to infestations in occurrence of disturbance, due to wind-felled, weakened or stressed trees, which commonly are not removed because of protection laws (Komonen et al. 2011; Schlyter & Lundgren 1993; Schroeder & Lindelöw 2002). Hence, commercial forests adjacent to conservation areas, may suffer from a higher risk of infestations compared to forests further away (Becker 1999; Zolubas & Dagilius 2012). However, conservation areas do not contribute to large-scale outbreaks of the spruce bark beetle in general (Schroeder & Weslien 2020), the spatial distribution of infestations regardless management type are suggested to strongly increase the risk of new infestations locally and in nearby surrounding forests the following year (commonly within 500 m during outbreaks; Kautz et al. 2011; Wichmann & Ravn 2001). Likewise, forest structure such as tree species composition, tree age and spruce tree density, can have a direct impact on the infestation probability (Overbeck & Schmidt 2012; Kärvemo et al. 2014; Kärvemo et al. 2016).

The European spruce bark beetle is not only a forest pest, but is also known to be an ecosystem engineer, a keystone species for establish important habitats for other species by creating succession disturbances and initiating wood decomposition (Müller et al. 2008). After a bark beetle attack, the killed spruce trees remain in conservation areas and form so-called "skeleton forests" (Müller et al. 2008). Skeleton forests leave a favourable environment with decaying wood, promoting biodiversity (Jonsell et al. 1998; Siitonen 2001; Stokland et al. 2012).

On the other hand, vital old spruce stands may be valuable for other species (Berg et al. 1994; Framstad 2013; Kärvemo et al. 2021). This makes skeleton forests ambiguous, by both being advantageous and disadvantageous in different scenarios. Fortunately, the spruce bark beetle has many known species of natural enemies, both predators and parasitoids, which can lower the spruce bark beetles productivity and can act as a natural pest-control (Lawson et al. 1996; Wegensteiner et al. 2015; Weslien 1992). The enemies are attracted by bark beetle pheromones and host-tree volatiles (Schroeder & Lindelöw 1989; Schroeder & Weslien 1994), and therefore tend to migrate to areas with high prey density (Weslien & Schroeder 1999). Several enemy species have been found to have a higher presence in unmanaged forests compared to managed forests (Weslien & Schroeder 1999). The reason for this is believed to be forest management being more harmful to the natural enemies, than the actual targeted spruce bark beetle (Weslien & Schroeder 1999; Weslien et al. 2022). However, the difference in enemy abundance between management types does not remain constant, as other studies have found no clear differentiation between managed and unmanaged forests, and in some cases even higher presence in managed forests of some enemy species (Hilszczański et al. 2007; Schlyter & Lundgren 1993).

1.3 Study purpose and hypotheses

The aim of this study was to improve our understanding about the influence of conservation areas regarding the spruce bark beetle's population dynamics, natural enemies, and biodiversity, during an outbreak in southern Sweden. I did this by investigating how managed forests, and two types of conservation areas, woodland key-habitats and nature reserves, differed in (i) spruce bark beetle attack density, offspring production, and reproductive success, along with (ii) abundance of natural enemies, and (iii) species richness of arthropods within the bark. In addition, I analysed their association to one another and to differences in the landscape and forest environment.

I hypothesized that a larger amount of killed trees will remain in conservation areas (mainly nature reserves) compared to the managed forests, because of no tree removal in conservation areas. Additionally, I expected a higher attack density in conservation areas and thus a higher offspring production, hence lower reproductive success in conservation areas, due to intraspecific competition. I also hypothesized higher species richness and higher abundance of natural enemies in conservation areas, based on conservation areas possibly having more favourable environment with dead wood and no harmful active pest-control.

2. Methods

2.1 Life cycle of the spruce bark beetle

In Sweden, spruce bark beetles (mainly adults) hibernate in the ground or under the bark during the winter and usually starts its swarming period in April/May (Hedgren & Schroeder 2004; Öhrn et al. 2014), when temperatures rise above approximately 17 ºC (Wermelinger 2004). Males start flying to search for a suitable host-tree with a diameter of at least 10 cm at breast height (Hedgren & Schroeder 2004), but preferable larger mature spruces (Holsten et al. 1989). The male bores an entrance hole through the bark and excavates a nuptial chamber, and thereafter excretes a pheromone to attract conspecifics (Hedgren & Schroeder 2004). Commonly, two or three females will enter, and mate with the male, but even up to five females can be achieved by the male (Hedgren & Schroeder 2004; Schlyter & Zhang 1996). After mating, each female excavates a maternal gallery vertically in the phloem and lays up to 80 eggs (Schlyter & Zhang 1996). After the eggs hatch, the larvae feed of the surrounding phloem, then turn into a pupa, and eventually develop into an adult and emerge from the tree, usually in July (Öhrn et al. 2014). The spruce bark beetle normally has only one generation per year in Sweden (Hedgren & Schroeder 2004), however, many of the parental beetles re-emerge and repeat the process (and produce sister broods) in another tree nearby (Öhrn et al. 2014). In addition, during extreme warm summers the spruce bark beetle can develop two generations during one year, such as 2006 and 2018.

2.2 Study area

The study was conducted in southern Sweden within the region of Götaland. The sampling was done during the autumn (October - November) each year from 2020 to 2022 (Figure 1). Each site had three forest locations grouped together in a triplet, where each triplet contained one managed forest, one woodland key-habitat, and one nature reserve (Figure 1). This was in order to have replicates of all three management types, within the same area and somewhat the same environmental conditions. The mean distance between the three forest locations within a triplet, was approximately 7 km. In total, 13 triplets were sampled, 4 triplets in 2020, 5 triplets in 2021, and 4 triplets in 2022 (Figure 1).

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Figure 1. Map of study area, zoomed-out (left) and zoomed-in (right). Displays all forest locations in triplets sampled between 2020-2022. Management type described as symbols, circle = managed forest, square = woodland key-habitat, and triangle = nature reserve.

2.2.1 Conservation areas

Nature reserves and woodland key-habitat are examples of conservation areas with a different degree of protection. Nature reserves are established to preserve valuable nature, protect species, and contribute to knowledge and human outdoor recreation (Naturvårdsverket 2023b). In Sweden, nature reserves are commonly owned by the state, or in some cases privately owned, and are usually large-scale conservation areas (Naturvårdsverket 2023c). Nature reserves are strictly protected by law and are operated by the county board in Sweden (Naturvårdsverket 2023c). Woodland key-habitats are usually small-scale conservation areas (around 3-5 ha) with hotspots of biodiversity (Timonen et al. 2011), and are in many cases a rare habitat often containing species of conservation interest (Timonen et al. 2011; Kärvemo et al. 2021). In Sweden, woodland key-habitats do not necessarily have legal protection (if not within a protected area), instead they are voluntary protected by land owners often incentivized by forest certification (Timonen et al. 2010). Hence, it is not illegal for the land owner to harvest or manage a woodland key-habitat

(Naturskyddsföreningen 2023). However, consultation with The Swedish Forestry Agency must be done beforehand (Skogsstyrelsen 2023).

In this study the nature reserves named, 2020; Huluskogen, Kattehålet, Skams hål, Taberg, 2021; Grimmestorp, Jättadalen-Öglunda, Ruderskogen, Råbyskogen, Stortorp, 2022; Karsmossen, Stora Fjället, Sydbillingen, Vristulven, were sampled. The nature reserves were initially visited, selected and sampled in the field, considering nature reserves being a less common conservation area. Thereafter, nearby woodland key-habitats and managed forests was visited, selected and sampled. The sampled conservation areas were required to contain at least 1 ha with over 200 m^3 spruce, because of the increasing probability of finding infested spruce trees to sample. Furthermore, this may in turn have caused bias, by increasing the probability of more local infested forest in the sampled conservation areas.

2.3 Sampling method

In total, 190 bark samples were collected from standing trees within 13 managed forests, 13 woodland key-habitats, and 13 nature reserves (Figure 1). Separately, in 2020 there were totally 54 samples collected from 4 forests of each management type (managed forest, woodland key-habitat, and nature reserve), in 2021 there were totally 78 samples collected from 5 forests of each management type, and in 2022 there were totally 58 samples collected from 4 forests of each management type (Figure 1). In each forest location, ideally 5 bark samples were collected of standing bark beetle infested spruce trees, and all bark samples per site were collected within approximately 100 m radius. The bark samples were cut out (ca. 15 x 45 cm) from the tree stem about 3 m above ground, and the tree diameter was noted and measured at breast-height.

The bark samples were transported to Uppsala, Sweden and refrigerated at the Swedish University of Agricultural Sciences, awaiting analysis. In the laboratory, each bark sample was measured (length and width) and all of the spruce bark beetles' egg galleries and hatch holes were recorded. Thereafter, each bark sample was torn apart into small pieces and carefully strained by hand. When straining, all spruce bark beetles (imago, pupae, and larvae) and all other arthropods were collected and counted. All species were sorted, noted, and stored in glass jars.

The bark samples from 2020 collected by Simon Kärvemo and the samples from 2021 were sampled by Simon and Pontus Eriksson, and all samples from 2020-2021 were reviewed by Pontus alone. The bark samples from 2022 were collected by me (Evelina Andersson), Hanna Jonsell and Simon, and later reviewed by me alone.

2.4 Geospatial data

To get a better understanding how large-scale factors (hereafter landscape factors) affect the spruce bark beetles population dynamics, its natural enemies and the species richness, several landscape variables were included in this study through remote sensing. On a local scale of 100 m radius, the variables spruce volume, birch volume, soil moisture, and amount infested forest were included, and on a regional scale of 1000 m radius, the total amount of area conserved was included.

2.4.1 Tree volume data

Forests with a higher volume of Norway spruce tend to increase the connectivity and colonization probability, and decrease the extinction probability of the spruce bark beetles' infestation patches (Kärvemo et al. 2014; Kärvemo et al. 2016). However, the non-host deciduous tree birch (*Betula spp.*) has been found to decrease the colonization probability (Byers et al. 1998; Kärvemo et al. 2014; Kärvemo et al. 2016; Schiebe et al. 2011; Zhang & Schlyter 2004). Birch leaves emit a chemical odour which reduces the attraction of bark beetles (Byers et al. 1998; Schiebe et al. 2011; Zhang & Schlyter 2004), possibly by avoiding wasting time searching for a host-tree (Byers et al. 1998). Hence, spruce volume and birch volume were included in this study.

Data of spruce volume and birch volume were accessed from the SLU Forest Map (2015). The data is created through co-processing from satellite images (Sentinel-2), and field data recording by the Swedish National Forest Inventory (Reese et al. 2003). The data consisted of two raster layers (one with spruce and one with birch) with a resolution of 12.5 x 12.5 m, but aggregated to 100 x 100 m by averaging. Each raster pixel showed the m^3/ha of spruce respectively birch, and the variables spruce volume and birch volume were calculated as the sum of pixels within 100 m radius, separately. Only the frequency of pixels with spruce volume >200 m^3/ha and birch volume >25 m^3/ha were included. This is according to a previous study by Kärvemo et al. 2014, which showed an increase in risk of spruce bark beetle infestation up to approximately 200 m^3/ha spruce, and then the risk levelled out (Kärvemo et al. 2014). Kärvemo et al. (2014) also found a peak in infestation risk when birch volume was about 25 m^3/ha, and thereafter the risk instead started to decrease (Kärvemo et al. 2014).

2.4.2 Soil moisture data

The soil moisture data was accessed from the SLU Soil moisture map (Ågren et al. 2021), and consisted of one raster layer with a resolution of 2 x 2 m. The soil moisture data is based on a LIDAR-derived terrain index (Ågren et al. 2021), showing predictions of soil moisture from dry to wet with a continuous index from 0 up to 100. Low index indicates dry soil, and with gradually increasing index it indicates mesic soil, mesic-moist soil, moist soil and wet soil, as it increases up to 100. In this study the soil moisture is the calculated mean of all pixel values within the 100 m radius. Only pixel values of <98 were included, considering values over 97 have a high probability to indicate bodies of water.

2.4.3 Infestation data

Data of locally bark-beetle killed tree stands (only trees killed from previous years), expressed as local infested forest, were included as a landscape variable. Data was assessed from high-resolution Sentinel-2 satellite images of bark beetle infestations with a new vegetation index: Distance Red SWIR (DRS). The DRS index has been shown to identify forest attacked by spruce bark beetle with at least 77% total accuracy (Persson et al. in prep). The data consisted of raster layers with a resolution of 10 x 10 m. The local infested forest is defined by the area (ha) of killed trees within 100 m radius. Our collected bark samples have the satellite data of the infested forest from the year before and earlier. i.e., the sampled bark from 2020 have satellite data from 2019 and earlier years, sampled bark from 2021 have satellite data from 2020 and earlier years, and sampled bark from 2022 have satellite data from 2021 and earlier years.

2.4.4 Conservation area data

The total area conserved within the landscapes was included as a variable to control for nearby conserved forest and the quantity of conserved area, for respective management. The data of conserved areas includes nature reserves, accessed through The Swedish Environmental Protection Agency (2023), and woodland key-habitats, accessed through The Swedish National Forest Inventory (2023), consisting of shape layers containing polygons of all Sweden's conserved areas. The total area conserved is the area sum of both nature reserves and woodland key-habitats within 1000 m radius, including the area of the possibly sampled conservation area.

Remote sensing method

To obtain data for each forest location, the computer program QGIS was used for remote sensing (QGIS Development Team 2023). The GPS-coordinates from each forest location were transmitted into QGIS and used as starting points. Thenceforward, to obtain the data for the local variables, a buffer zone was created with the tool “Fixed distance buffer”, with a 100 m radius from each GPS-point. The tool “clip raster by mask layer” was later used to only retain the pixels within the buffer. To extract the value from each pixel, the tool “Raster pixels to points” was first used and then the tool “Show statistical summary” to get the number of points (pixels) or mean value of all the points (pixels) within the buffer. For the regional landscape variable, total area conserved, instead got a buffer zone with a 1000 m radius from each GPS-point. The tool “clip vector layer by mask layer” was used on the nature reserve polygons, respectively woodland key-habitat polygons. This created new layers containing the nature reserves and woodland key-habitats remaining within 1000 m. Thereafter a new column was made in the attribute table with the sum of the area ha of nature reserves respectively woodland key-habitats. Lastly, the nature reserve area and woodland key-habitat area were summed up together to get the total area conserved within 1000 m of each forest location.

This remote sensing method was done for all forest locations 2020-2022, and all performed by me (Evelina Andersson) alone.

2.5 Statistical analyses

After excluding dry bark samples with almost no arthropod content, believed to be from a previous attack year and sampled by mistake, a total of 160 bark samples were used in the statistical analysing. Because the data from several trees was sampled within different sites, the statistical analysis requires taking this in consideration and using the site as a random factor. All tests done in the statistical analysis were additionally tested with multiple comparisons tests, to compare between the three management types.

To test the difference in the environmental response variables tree diameter, spruce volume, birch volume, soil moisture, infested forest, and area conserved between managements, the first following model was constructed. Model 1: [Response variable ~ Management + (1|site)]. For the non-count response variable tree diameter (which model residuals was normally distributed by logarithm) a Linear Mixed-Effects Models (LMM) test was used with Model 1, to test the difference between managements. For the non-count response variable soil moisture (which model residuals was not normal distributed) a Kruskal-Wallis test was used with Model 1, to tests the difference between managements. However, because of the appropriate test for soil moisture, the site could not be included as a random factor when testing soil moisture, so (1|site) was excluded from the model in this case. To test the difference in each one of the response variables spruce volume, birch volume, infested forest, and area conserved between managements, Model 1 was used for each response variable separately and tested separately with a Negative Binomial Generalized Linear Mixed-Effects Model (GLMM), as the models were overdispersed and thus had a better fit with a negative binomial distribution.

The bark samples were not equal in size, consequently the bark data was put in proportion by including an offset with bark size in the following model to compare per m^2. Model 2: [Response variable ~ Management + (1|site) + offset(log(size))].

To test the difference in the response variable species richness between managements, Model 2 was used and tested with a GLMM with family Poisson, since the data was not overdispersed.

The groups of natural enemies included in this study were: *Medetera*, parasitoids, *Plegaderus*, Staphylinidae, Cecidomyiidae, Sciaridae, *Thanasimus, Lonchaea*, Stratiomyidae, *Rhizophagus*, and Raphidiidae. The total number of natural enemies included the total counts of all the previous mentioned enemy groups. To test the difference in the response variables *Medetera*, parasitoids, *Plegaderus*, Staphylinidae, Cecidomyiidae, and Sciaridae between managements, Model 2 was used for each response variable separately and tested separately with a Negative Binomial GLMM, due to overdispersion. However, the less important *Thanasimus*, *Lonchaea*, Stratiomyidae, *Rhizophagus*, and Raphidiidae were excluded when the groups of natural enemies were tested separately, due to lack of data or overfitted data, and thus not converging when tested. Further, to test the difference in the total number of natural enemies (groups pooled together) between managements, Model 2 was used and also tested with a Negative Binomial GLMM due to overdispersion.

In this study three response variables were used to describe the population dynamics of the spruce bark beetle: attack density, offspring production and reproductive success. The attack density of spruce bark beetles equals the number of egg galleries per m^2 bark, and the offspring production is the sum of produced offspring beetles: [number of juvenile beetles + hatch holes] per m^2 bark. Reproductive success is the calculated number of daughters per mother beetle: [number of produced beetles x 0.5] / [number of egg galleries] (Hedgren & Schroeder 2004). The pupae and larvae were not included as they contributed to a minor part (17%) of produced offspring, and have a very low probability of surviving hibernation (Annila 1969). To test the difference in attack density and offspring production between managements, Model 2 was separately used for the response variables and separately tested with a Negative Binomial GLMM, as the data were overdispersed. However, because reproductive success was defined as the number of daughters per mother beetle and not compared per m^2 bark, Model 2 with the size offset could not be used. Further, to test the difference in reproductive success between managements, Model 1 was used and tested with a Generalized Linear Mixed-Effects Model with family Poisson, as the data was not overdispersed.

Previously during this statistical analysis, it showed a difference in the amount of local infested forest between managements. Because of this I also wanted to control for population pressure when analysing the population dynamics, this by constructing the following models. Model 3: [Response variable ~ Management + (1|site) + offset(log(size)) + offset(log(local infested forest + 1))] for the response variables attack density, and offspring production. Additionally, Model 4:

[Response variable ~ Management + (1|site) + offset(log(local infested forest + 1))] for the response variable reproductive success, without the size offset. Each one of the response variables were tested separately, with the same tests as previously.

All analyses were conducted in R version 4.2.3 (R Core Team, 2023), using the packages blmeco for checking data dispersion (Korner-Nievergelt et al. 2015), lme4 for GLMM and LMM tests (Bates et al. 2015), multcomp (for multiple comparisons of LMM and GLMM tests) and dunn.test (for Kruskal-Wallis test) for multiple comparisons and adjusted p-values (Hothorn et al. 2008; Dinno 2017), and ggplot2 for constructing plots (Wickham 2016).

3. Results

3.1 Environment

Statistics of the following results can be found in Appendix 1, Appendix 2, and associated graph in Appendix 3. The tree diameter of the sampled spruce trees was generally larger in conservation areas compared to managed forests, and more similar between nature reserves and woodland key-habitats. Managed forest trees had a mean diameter of 29.6 cm, woodland key-habitats a mean of 35.4 cm, and nature reserves a mean of 33.5 cm in tree diameter. Additionally, nature reserves had 112% more spruce, and woodland key-habitats 83% more spruce, compared to managed forests. However, there was no difference in spruce volume between nature reserves and woodland key-habitats. Nature reserves had generally 40% less birch, and woodland key-habitats 65% less birch, compared to managed forests. In addition, nature reserves had 74% more birch than woodland key-habitats. Regarding soil moisture, woodland key-habitats were 58% drier, and nature reserves 36% drier, compared to the managed forests soil moisture. But there was no difference in soil moisture between conservation areas. Furthermore, nature reserves turned out to have generally 15% more, and woodland key-habitats 85% more area of infested forest locally, compared to managed forests. Yet, no difference in area of local infested forest between woodland key-habitats and nature reserves was found. Further, all three management types differed from each other in the total area conserved in the surrounding landscape. Nature reserves had most, a mean of 88.2 ha conserved, woodland key-habitats less with a mean of 9.2 ha conserved, and managed forests the least, with a mean of 3.8 ha conserved in the surrounding landscape.

Table 1. Units, means ± SD, and ranges of species richness, natural enemies, and population dynamics, in respective management. The units with m^2 refers to m^2 bark.

		Managed forests		Woodland key-habitats		Nature reserves	
Variable	Unit	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Species richness							
Arthropod species	number/m^2	152 ± 48	51.6 - 374	153 ± 52.5	74.1 - 344	169 ± 57.2	74.1 - 324
Natural enemies							
Medetera	number/m^2	354 ± 336	0 - 1879	437 ± 295	0 - 1413	491 ± 402	11.5 - 1676
Parasitoids	number/m^2	61.4 ± 101	0 - 560	51.8 ± 91.5	0 - 580	108 ± 259	0 - 1471
Thanasimus	number/m^2	3.2 ± 9	0 - 46.8	2.1 ± 5.7	0 - 28.7	2.1 ± 7.2	0 - 42.9
Plegaderus	number/m^2	21.8 ± 33.8	0 - 174	36.8 ± 69.5	0 - 340	55.3 ± 77.8	0 - 364
Lonchaea	number/m^2	16.8 ± 34.2	0 - 171	11.3 ± 31.6	0 - 186	6.7 ± 14	0 - 60.9
Staphylinidae	number/m^2	42.1 ± 48	0 - 210	66.4 ± 77.3	0 - 421	73.4 ± 93.7	0 - 449
Stratiomyidae	number/m^2	59.7 ± 97.8	0 - 614	61.4 ± 121	0 - 634	122 ± 351	0 - 2122
Cecidomyiidae	number/m^2	51.5 ± 102	0 - 569	126 ± 297	0 - 1646	173 ± 259	0 - 1398
Sciaridae	number/m^2	603 ± 1657	0 - 9057	282 ± 758	0 - 4740	512 ± 1238	0 - 5986
Rhizophagus	number/m^2	5.8 ± 13.9	0 - 62.4	11.4 ± 33.2	0 - 190	7 ± 27.6	0 - 178
Raphidiidae	number/m^2	0.2 ± 1.6	0 - 12.3	1.3 ± 4.1	0 - 14.3	0.6 ± 2.9	0 - 14.8
Total enemies	number/m^2	1220 ± 1803	56.1 - 9591	1088 ± 945	119 - 5474	1551 ± 1501	104 - 8306
Population dynamics							
Attack density	no. egg galleries/m^2	291 ± 187	14.2 - 874	304 ± 106	64.5 - 570	320 ± 189	11.5 - 887
Offspring production	no. offspring beetles/m^2	451 ± 345	58.3 - 1989	702 ± 745	0 - 2667	563 ± 423	11.5 - 1578
Reproductive success	no. daughters/mother beetle	1 ± 0.8	0.1 - 3.5	1.2 ± 1.2	0 - 5.5	1.1 ± 1	0.1 – 4.3

3.2 Species richness

There was a higher species richness per m^2 bark in nature reserves, compared to managed forests (Table 1, Table 2, Figure 2). However, there was no difference in the number of species per m^2 between nature reserves and woodland key-habitats, or between woodland key-habitats and managed forests (Table 1, Table 2, Figure 2).

Table 2. Outputs of test with Model 2 and multiple comparisons of species richness between managements per m^2 bark. M = managed forests, WKH = woodland key-habitats, NR = nature reserves. The p-values are adjusted for multiple tests. For units, means ± SD, and ranges of variable see Table 1.

Variable	Estimate	SE	p-value
Species richness			
WKH - M	0.03646	0.05877	0.535
NR - M	0.12788	0.05748	**0.026**
NR - WKH	0.09141	0.06042	0.130

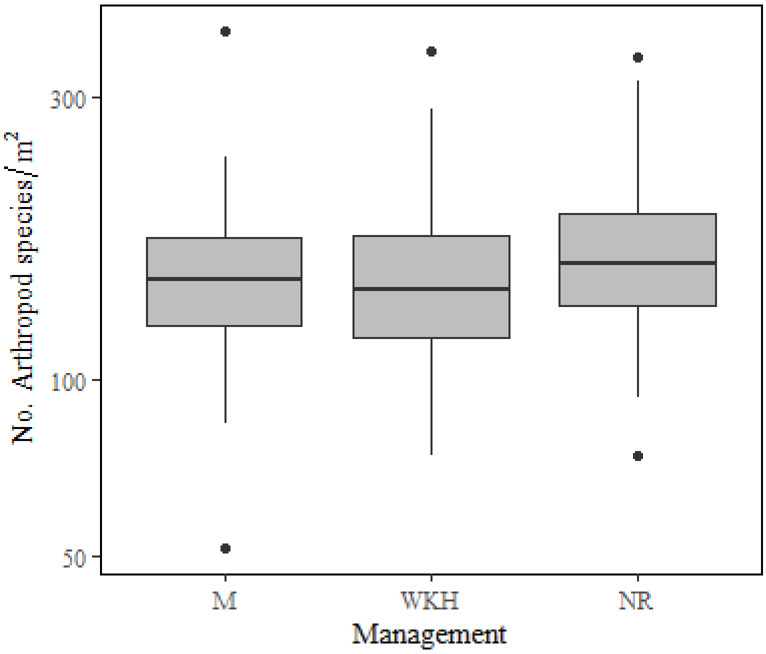

Figure 2. Boxplot of the species richness of arthropods per m^2 bark in each management. X-axis shows managements as; M = managed forests, WKH = woodland key-habitats, NR = nature reserves. Bar: median; box: interquartile range (IQR); whiskers: min/max. values < 1.5 × IQR below/above box; dots: outliers.

3.3 Natural enemies

When looking at the number of natural enemies per m^2 bark, separated by group, there was a higher density of *Medetera*, *Plegaderus*, Staphylinidae, and Cecidomyiidae in nature reserves compared to managed forests (Table 1, Table 3, Figure 3). But parasitoids, and Sciaridae occurred to be in a similar density between nature reserves and managed forests (Table 1, Table 3, Figure 3). A higher density of Staphylinidae, and Cecidomyiidae was found, and an indication of more *Medetera*, in woodland key-habitats, compared to managed forests. However, a comparable density of *Plegaderus*, parasitoids, and Sciaridae between woodland key-habitats and managed forests (Table 1, Table 3, Figure 3). Between woodland key-habitats and nature reserves, there was a higher density of parasitoids, Sciaridae, and an indication of more *Plegaderus*, in nature reserves. Yet a similar density of *Medetera*, Staphylinidae, and Cecidomyiidae between woodland key-habitats and nature reserves per m^2 (Table 1, Table 3, Figure 3).

The total number of enemies (enemy groups pooled together) per m^2 bark, was higher in nature reserves in comparison to both woodland key-habitats and managed forests (Table 1, Table 3, Figure 3). Although the woodland key-habitats and managed forests had a comparable abundance of total enemies (Table 1, Table 3, Figure 3).

Table 3. Outputs of tests using Model 2 and multiple comparisons in natural enemies between managements, per m^2 bark. M = managed forests, WKH = woodland key-habitats, NR = nature reserves. The p-values are adjusted for multiple tests. For units, means ± SD, and ranges of variables see Table 1.

Variable	Estimate	SE	p-value
Medetera			
WKH - M	0.26539	0.15275	0.082
NR - M	0.35867	0.15439	**0.020**
NR - WKH	0.09328	0.16284	0.567
Parasitoids			
WKH - M	-0.1846	0.312	0.554
NR - M	0.5282	0.3396	0.120
NR - WKH	0.7128	0.3409	**0.037**
Plegaderus			
WKH - M	0.4458	0.3082	0.148
NR - M	1.0790	0.3146	**<0.001**
NR - WKH	0.6332	0.3317	0.056
Staphylinidae			
WKH - M	0.51365	0.19368	**0.008**
NR - M	0.5945	0.1975	**0.003**
NR - WKH	0.08085	0.20167	0.689
Cecidomyiidae			
WKH - M	0.8942	0.3506	**0.011**
NR - M	1.1773	0.3439	**<0.001**
NR - WKH	0.2831	0.3626	0.435
Sciaridae			
WKH - M	-0.5283	0.4488	0.239
NR - M	0.4785	0.4734	0.312
NR - WKH	1.0068	0.4303	**0.019**
Total enemies			
WKH - M	0.02668	0.16431	0.871
NR - M	0.42537	0.16918	**0.012**
NR - WKH	0.39869	0.16793	**0.018**

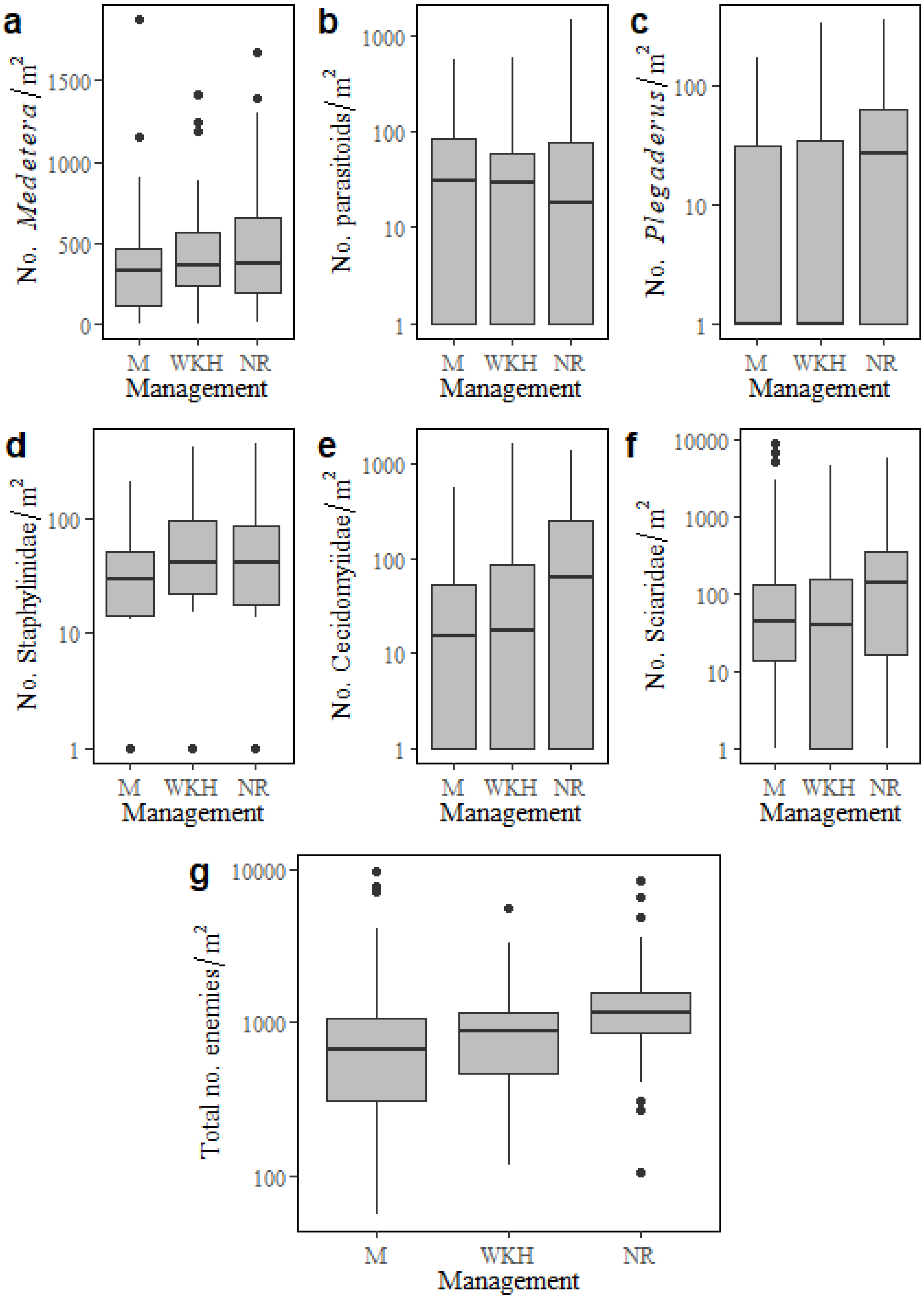

Figure 3. Boxplots of the number of natural enemies per m^2 bark in each management, M = managed forests, WKH = woodland key-habitats, NR = nature reserves. The boxplots show the number of (a) Medetera, (b) parasitoids, (c) Plegaderus, (d) Staphylinidae, (e) Cecidomyiidae, (f) Sciaridae, and (g) total enemies. Bar: median; box: interquartile range (IQR); whiskers: min/max. values < 1.5 × IQR below/above box; dots: outliers. In boxplot b, c, d, e, f, and g, all values are +1, to be able to perform logarithm for better visual display.

3.4 Population dynamics

Without considering the differences in amount of local infested forest between managements (Appendix 2), there was no difference found in either attack density or reproductive success of the spruce bark beetle, between the managements (Table 1, Table 4, Figure 4). In contrast, the offspring production of the spruce bark beetle was found to be higher in woodland key-habitats, compared to managed forests, but not in the other cases (Table 1, Table 4, Figure 4). However, when the differentiation in local infested forest was taken into consideration and controlling for the amount of killed spruce trees locally (population pressure), it showed a lower reproductive success, and indication of lower attack density, in nature reserves compared to managed forests (Table 4). But, similar offspring production between managed forests and nature reserves (Table 4). There was a lower attack density, lower offspring production, and lower reproductive success of the spruce bark beetle in woodland key-habitats compared to managed forests (Table 4), while there was a higher reproductive success in nature reserves compared to woodland key-habitats (Table 4). Contrary, no difference in either attack density or offspring production between conservation areas (Table 4).

Table 4. Outputs of tests with the different models, and multiple comparisons of population dynamics between managements. M = managed forests, WKH = woodland key-habitats, NR = nature reserves. The p-values are adjusted for multiple tests. For units, means ± SD, and ranges of variables see Table 1.

Variable	Estimate	SE	p-value
Attack density			
Model 2			
WKH - M	0.13129	0.0937	0.161
NR - M	0.11514	0.0941	0.221
NR - WKH	-0.01616	0.0988	0.870
Model 3			
WKH - M	-0.5498	0.1753	**0.002**
NR - M	-0.3626	0.1962	0.065
NR - WKH	0.1872	0.203	0.356
Offspring production			
Model 2			
WKH - M	0.3251	0.1607	**0.043**
NR - M	0.1421	0.1589	0.371
NR - WKH	-0.1829	0.1634	0.263
Model 3			
WKH - M	-0.4467	0.197	**0.023**
NR - M	-0.1611	0.2255	0.475
NR - WKH	0.2856	0.2305	0.215
Reproductive success			
Model 1			
WKH - M	0.07486	0.18270	0.682
NR - M	0.03127	0.18555	0.866
NR - WKH	-0.04359	0.18944	0.818
Model 4			
WKH - M	-1.0786	0.2063	**<0.001**
NR - M	-0.5894	0.2100	**0.005**
NR - WKH	0.4892	0.2177	**0.025**

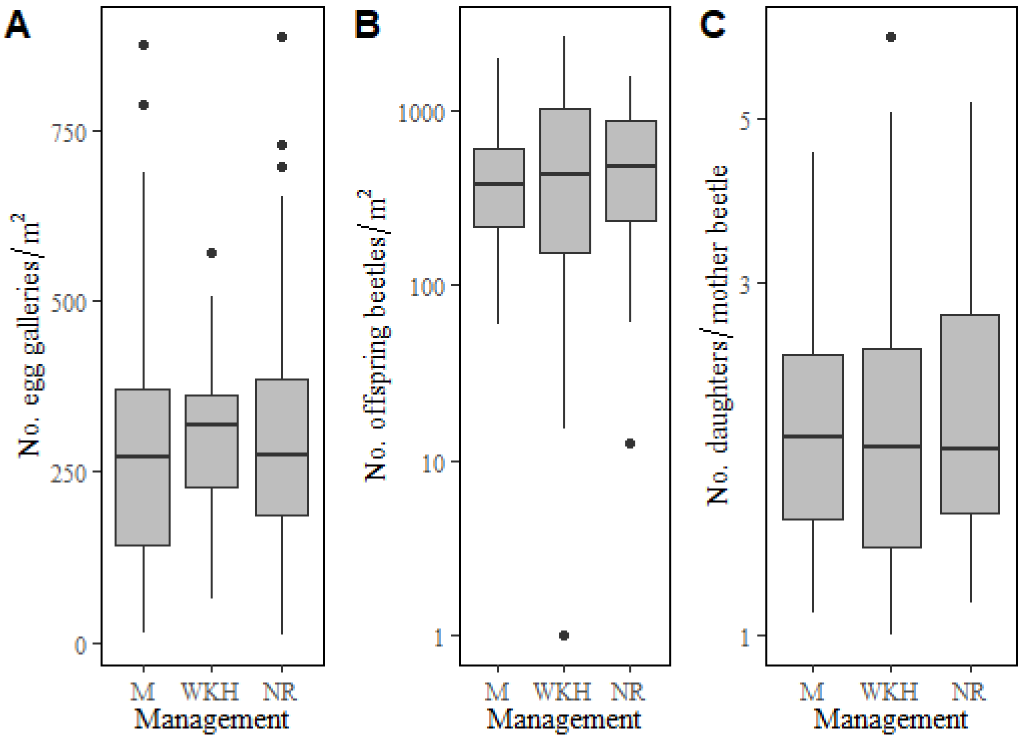

Figure 4. Boxplot of (A) attack density, (B) offspring production, and (C) reproductive success within the bark, in the different managements, M = managed forests, WKH = woodland key-habitats, NR = nature reserves. Bar: median; box: interquartile range (IQR); whiskers: min/max. values < 1.5 × IQR below/above box; dots: outliers. In boxplot B, and C, all values are +1, to be able to perform logarithm for better visual display.

4. Discussion

4.1 Environment

In summary, conservation areas had generally more and larger spruce trees, less birch content, drier soil, and more infested forest locally, along with more area conserved in their surrounding landscape, compared to managed forests. However, nature reserves had more birch content locally, and more area conserved in the surrounding landscape than woodland key-habitats.

Historically, the forest industry is known to plant spruce monoculture and practice forest ditching and drainage to increase the land's suitability for timber production (Felton et al. 2010a; Laine et al. 1995). Managed forests, i.e., commercial forests, are therefore expected to have more spruce, and a lower soil moisture (Felton et al. 2010a; Laine et al. 1995). Surprisingly, the results from the managed forest sites in this study showed the opposite of this (Appendix 1, Appendix 2, Appendix 3). However, the fact that conservation areas generally had more spruce compared to managed forests, may have been caused by actively selecting nature reserves and woodland key-habitats with a high spruce content (see Conservation areas 2.2.1). The higher spruce volume can further explain why the conservation areas generally had less birch content than managed forests. The conservation areas in this study having a generally larger amount of local infested forest could partly be explained by our method of selecting conservation areas with a high probability of infestation (see Conservation areas 2.2.1), which may have increased the amount. However, the drier soil in the conservation areas might also explain why the local infested forest were generally more pronounced in conservation areas, considering drought causing stress in standing trees and reduce bark beetle performance and thus more vulnerable for attacks (Marini et al. 2017; Netherer et al. 2021). Additionally, drought tends to trigger the spruce bark beetles' symbiotic ophiostomatoid fungi to produce beetle semiochemicals and detoxify tree defence compounds (Netherer et al. 2021). Also, given that conservation areas generally had larger spruce trees may have increased the infestations, considering that spruce bark beetles prefer mature spruce trees (Holsten et al. 1989; Overbeck & Schmidt 2012; Müller et al. 2022). Moreover, conserved spruce dominated forests having larger areas with killed trees, agrees with the hypothesis, considering no management allowed versus a smaller amount of killed trees in managed forests, where thinning and logging are common practice to inhibit infestation (Lindelöw & Schroeder 2008). Nature reserves having the largest area conserved in the landscape, and woodland key-habitats the second most, are consistent with the average sizes of respective management in Sweden (woodland key-habitat = small-scale conservation, and nature reserve = large-scale conservation). Managed forests having the least conserved area in the surrounding landscape is accurate regarding the sampled managed forests were not by themselves within a conservation area and the majority of their regional landscape probably consist of silviculture.

4.2 Species richness

The results showed a higher species richness in nature reserves compared to managed forests, which agrees with my hypothesis. Also, this were in agreement with the hypothesis of having a higher species richness in areas with a higher amount of dead wood, which nature reserves had compared to managed forests (Djupström et al. 2008). Additionally, nature reserves having generally more and larger spruce trees (i.e., older mature spruce trees), may also have contributed to higher species richness (Berg et al. 1994; Framstad 2013; Kärvemo et al. 2021). However, despite woodland key-habitats also having more dead wood than managed forests they did not have more species in comparison, which do not agree with my hypothesis. Woodland key-habitats not having more species could possibly partly depend on containing less birch than the nature reserves, considering spruce-birch mixtures generates higher biodiversity (Felton et al. 2010b; Felton et al. 2016). These differences indicate a positive relationship between killed trees and species richness with larger population sizes of individual species (lower risk for local extinction) that increases with the amount of new (and old) dead wood (Siitonen 2001), and between species richness and habitat diversity (mixed forest = more different niches) (Felton et al. 2010b; Jonsell et al. 1998). Hence, the size of the conservation area, including more dead woods, might be the strongest predictor regards species richness, considering nature reserves having significantly larger areas conserved in the landscape than woodland key-habitats. Also, if several patches of larger conserved forest are available in the regional landscape, they could function as stepping stones for the species living in the nature reserve, escaping forestry (Fischer et al. 2006). Moreover, woodland key-habitats seems to have limited effect on conserving biodiversity, possibly by being small conserved patches, getting affected by surrounding silviculture giving edge-effects, isolation, poorer genetic viability and resulting in insubstantial species populations (Hanski 2005; Soulé & Terborgh 1999; Timonen et al. 2011).

4.3 Natural enemies

The abundance of natural enemies follows the general patterns of species richness to a high extent, and is consistent with the hypothesis of conservation areas having more natural enemies. Nature reserves had not only generally more natural enemies compared to managed forests, but also generally more compared to woodland key-habitats. More specific, nature reserves had higher densities of *Medetera*, *Plegaderus*, Staphylinidae, Cecidomyiidae, and total number of enemies, compared to managed forests. Nature reserves also had higher densities of parasitoids, Sciaridae, and total number of enemies, compared to woodland key-habitats. Additionally, woodland key-habitats had significantly higher densities of Staphylinidae, Cecidomyiidae, and an indication of more *Medetera*, compared to managed forests. More natural enemies in nature reserves could be related to the higher amount of stressed and killed trees in nature reserves, by sending out bark beetle pheromones and host-tree volatiles attracting enemies (Schroeder & Lindelöw 1989; Schroeder & Weslien 1994). Moreover, nature reserves being left untouched and having no active pest-control may create a favourable environment for the natural enemies, which likely are sensitive to certain types of forestry (Weslien & Schroeder 1999; Weslien et al. 2022). Furthermore, both conservation areas having more natural enemies than managed forests in some enemy groups, might have been caused by conservation areas having more remaining dead wood which may create sustainable enemy populations (Siitonen 2001). The reason nature reserves also generally had more natural enemies than woodland key-habitats, can similarly as the species richness, depend on woodland key-habitat being a small-scale conservation area and having less conserved area in the surrounding landscape, creating isolation and edge-effects from surrounding silviculture possibly resulting in insubstantial enemy populations (Hanski 2005; Soulé & Terborgh 1999; Timonen et al. 2011).

4.4 Population dynamics

Without controlling for the population pressure (amount of killed trees locally), the spruce bark beetles' attack density, offspring production, and reproductive success did not differ between nature reserves and managed forests, which are not consistent with my hypotheses. However, the results are supported by some previous studies, where managed forests and unmanaged forests have been found to not necessarily differentiate in bark beetle abundance (Hilszczański et al. 2007; Schlyter & Lundgren 1993; Weslien & Schroeder 1999). However, the results are interesting considering conservation areas had more spruce, less birch, drier soil and more local infested forest compared to managed forests, which typically results in higher attack densities (Kärvemo et al. 2014; Kärvemo et al. 2016; Müller et al.

2022; Wichmann & Ravn 2001). For all three management types, the attack density was around 300 egg galleries/m^2 bark, which are considered to be the upper limit in endemic populations (Furuta 1989). Moreover, the reproductive success was around 1 daughter per mother beetle in all three managements types, which is considered generally low (Weslien & Regnander 1990). Low attack density often results in high reproductive success because of less intraspecific competition, but that seems not to be the case in this study. The offspring production of the spruce bark beetle was higher in woodland key-habitats, compared to managed forests. This might be the outcome of woodland key-habitats having larger trees than managed forests (more breeding space) (Weslien & Regnander 1990), and lower species richness and densities of total natural enemies than nature reserves (low spruce bark beetle mortality and low competition), which gives a suitable breeding environment for the spruce bark beetles, resulting in a thriving production in woodland key-habitats.

When controlling for the population pressure (amount of killed trees locally), i.e., if the different managements would have had the same amount of infested forest, the results changed and managed forests had higher attack density, offspring production, and reproductive success of spruce bark beetles, compared to woodland key-habitats. Managed forests also had a marginally higher attack density, and significantly higher reproductive success compared to nature reserves. In conservation areas, because of more suitable host-trees (drought stress and more and larger spruce trees), the bark beetles can select host-tree more freely and the beetles can spread out over a larger number of trees, which dilutes the attack density. In managed forests there are fewer suitable host-trees, thus the spruce bark beetles have less alternatives, which gives a concentrated attack density depending on less breeding space and thereby successfully exceeding the attack threshold (Mulock & Christiansen 1986). Nature reserves having marginally lower attack density of spruce bark beetles than managed forests, could perhaps also be an effect of interspecific competition by nature reserves having a higher species richness resulting in less available space for egg galleries in the bark (Byers 1989). Further, managed forest having higher offspring production of spruce bark beetles than woodland key-habitats when controlling for population pressure are probably associated with the higher attack density in managed forests, i.e., more egg galleries yield more oviposition and *per se* results in more offspring per m^2 bark. Moreover, with similar population pressure, conservation areas had lower reproductive success of spruce bark beetles compared to managed forests. Nature reserves having generally more natural enemies and species should have contributed to this by interspecific competition and induced mortality of spruce bark beetles. Woodland key-habitats did however still have higher densities within some enemy groups than managed forests, e.g., marginally more *Medetera* which are one of the most important enemies of spruce bark beetles (Lawson et al. 1996; Wegensteiner et al.

2015), which could have resulted in higher beetle mortality and giving lower reproductive success. However, the effectiveness of natural enemies on bark beetle mortality are ambiguous and difficult to determine, considering this study did not directly test the enemy influence. However, the reason why the population dynamics functioned this way in the woodland key-habitats are unclear and are difficult to explain. Likewise, there are also difficult to explain why nature reserves had higher reproductive success than woodland key-habitats under similar population pressure. Yet, one possible explanation could be that nature reserves, unlike woodland key-habitats, are able to support sustainable species populations, i.e., even a sustainable spruce bark beetle population, because of more conserved area in the surrounding. Further, the results of the population dynamics give an indication of local infestation size being a strong predictor of the population dynamics, considering the significant change in results when controlling for population pressure. Additionally, even though nature reserves had more local infested forest originally, they did not have higher rates of spruce bark beetles, compared to managed forests. The similarities and later differences indicate that nature reserves (and woodland key-habitats under similar population pressure), do have natural control over their spruce bark beetle populations. In some means perhaps even more effective inhibition of the spruce bark beetle populations than managed forests, considering the differences in environment. This perhaps by having sustainable species and enemy populations, which managed forests are unable to have possibly because of the harming active pest-control. Further, previous studies have investigated what effect active pest-control versus non-intervention management have on spruce bark beetles inside conservation areas (Fora & Balog 2021; Vanická et al. 2020), and they found no distinct differentiation in the population dynamics of the spruce bark beetles between active pest-control and non-intervention management. This can further strengthen the suggestion of natural control being comparable in effectiveness to active pest-control regards the general population dynamics within a forest.

The indicating importance of leaving conservation areas unmanaged, still holds the question of possible connectivity and spread to the direct adjoined forests when not removing infested spruce trees (which was not within the scope of this study). Efficient prevention of spruce bark beetles spread to adjoining forests have been showed by creating phytosanitary protection zones around conservation areas (Angst et al. 2012; Ebregt & Greve 2000; Nikolov et al. 2014; Wermelinger 2004), with buffer zones of a few hundred meters in width (Angst et al. 2012; Nikolov et al. 2014; Wermelinger 2004). These buffer zones can e.g., be constructed to have absence of Norway spruce, and resulting in densities below high-risk thresholds of spreading beetles within a few hundred meters (Angst et al. 2012). In addition, this might be a possible implementation in future conservation efforts, to reduce the connectivity spread and make forest conservation less problematic. However, this may only be suitable in large-scale conservation areas considering the effective width size of the buffer zones.

4.5 Conclusions

In this study, nature reserves did not differ directly in rates of the spruce bark beetle compared to managed forests, but nature reserves did have some lower rates of spruce bark beetles under similar population pressure. Woodland key-habitats had directly higher offspring production compared to managed forests, but at the same time lower rates under similar population pressure. Moreover, nature reserves exclusively possessed the highest species richness and abundance of natural enemies in general. This likely by nature reserves having favourable habitats of decomposed wood initiated by spruce bark beetles, and nature reserves being a diverse unmanaged conservation area with the most area conserved in the surrounding landscape, creating sustainable species population with low risk of local extinction and give species the ability to escape harming active pest-control in the surrounding landscape. Accordingly, woodland key-habitats' smaller area conserved in the surroundings might be the main cause of insubstantial enemy and species populations, possibly contributing to the direct higher spruce bark beetle offspring production. This suggests that nature reserves are able to allow natural ecological processes and maintain vital ecosystem functioning among spruce bark beetles and their natural enemies, resulting in high biodiversity and a natural control with possibly relatively high spruce bark beetle mortality. However, the influence of woodland key-habitats is more unclear and remains to be addressed.

4.6 Limitations and future research

There were several more questions that could have been investigated and tested in this study, but in order to stay within the framework of this degree project, limitations were necessary. I would have wanted to involve enemies as predictors in the models for offspring production and reproductive success, to see how they affected the spruce bark beetles, and if specific enemy groups had more impact than others. Because the natural enemy's direct impact on spruce bark beetle mortality is still relatively unknown for some of the enemy groups. Furthermore, it would have been interesting to analyse the change over time, if there was a difference between the years 2020-2022. Considering, e.g., previous year enemy abundance might have an impact on next year spruce bark beetle population dynamics. Also, including a larger landscape perspective, by adding several buffer zones (e.g., 300 m, 500 m, 700 m) with landscape data (tree volume, soil moisture, infested forest) and not only 100 m radius, to be able to look at the impact of large-scale landscape composition. I would have liked to test and compare the managed forests with and without conserved areas within its region, to see if conserved areas nearby increase the attack density, if conservation areas nearby contribute to spread. In future studies it would have been interesting to look at the number of enemy species and perhaps also include the spruce bark beetle’s symbiotic ophiostomatoid fungi as a factor. Likewise, investigate this topic between managements when having similar tree composition and soil moisture.

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Populärvetenskaplig sammanfattning

För att nå Sveriges miljömål om levande skogar och ett rikt växt- och djurliv, måste mer omfattande bevarandeinsatser göras för att lyckas hejda förlusten av biologisk mångfald och viktiga livsmiljöer. Olyckligtvis har klimatförändringarnas bidragande till storskaliga utbrott av den träddödande granbarkborren gjort skogsbevarande kontroversiellt. Under utbrott kan ibland hela naturvårdsområden skadas, och därmed mista sitt syfte att skydda natur. Detta har dessutom gjort att naturvårdsområden ofta anklagats för att sprida granbarkborrar genom att eventuellt öka angrepp i omgivande produktionsskog. Emellertid är granbarkborren samtidigt känd för att främja biologisk mångfald genom att lämna gynnsamma miljöer med död ved. För att undvika utbrott av granbarkborre använder produktionsskog olika metoder av aktiv skadedjurskontroll, t.ex. gallring och avverkning. Dessa metoder har tvetydliga resultat och tros kunna påverka vissa andra arter mer negativt än själva granbarkborren. Naturvårdsområden, som bör lämnas orörda, måste istället förlita sig på granbarkborrarens naturliga fiender, vilka livnär sig på granbarkborren och därmed kan fungera som en typ av naturlig skadedjurskontroll. För att förbättra vår förståelse om skogliga naturvårdsområdens inverkan, jämförde denna studie hur granbarkborren, dess naturliga fiender och antal leddjursarter skiljer sig mellan naturreservat, nyckelbiotoper och produktionsskog under ett utbrott i södra Sverige. Resultaten visade att naturvårdsområdena i denna studie hade t.ex. torrare mark och mer gran än produktionsskog, vilket teoretiskt sett är en miljö mer benägen för angrepp. Men trots detta hade, i synnerhet naturreservat, inte högre nivåer av granbarkborren jämfört med produktionsskog. Dock påvisades en högre produktion av granbarkborrar i nyckelbiotoper än produktionsskog. Men under likande populationstryck hade naturvårdsområden till och med lägre nivåer av granbarkborren än produktionsskog. Naturreservat hade dessutom fler leddjursarter än produktionsskog, och även fler totalt antal naturliga fiender jämfört med både produktionsskog och nyckelbiotoper. Liknande eller lägre nivåer av granbarkborren tros bero på fler fiender och fler arter, och det i sin tur p.g.a. större bevarad orörd yta i landskapet och varierande miljö med död ved. Detta tyder på att naturreservat tillåter och upprätthåller naturliga och viktiga samspel mellan granbarkborren, dess naturliga fiender och andra arter, vilket resulterar i hög biologisk mångfald och möjligen en relativt effektiv naturlig skadedjurskontroll. Däremot är inverkan av nyckelbiotoper mer oklar och återstår att undersöka noggrannare.

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Appendix 1

Units, means ± SD, and ranges of all environmental variables used in this study, in respective management. Tree diameter refers to the sampled spruce trees. Local = within 100 m radius, and regional = within 1000 m radius.

Variable	Unit	Managed forests		Woodland key-habitats		Nature reserves	
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Environment							
Tree diameter	cm	29.6 ± 7.95	13 - 55	35.4 ± 10.3	22 - 60	33.5 ± 9.01	20 - 55
Local spruce volume	m^3/ha	0.42 ± 0.38	0 – 1.25	0.77 ± 0.45	0.09 – 1.57	0.89 ± 0.42	0.16 – 1.36
Local birch volume	m^3/ha	0.55 ± 0.29	0.2 – 1.25	0.19 ± 0.24	0.01 – 1.02	0.33 ± 0.24	0.07 – 0.77
Local soil moisture	index	27.7 ± 14.3	9.26 - 59.8	11.5 ± 10.9	2.15 - 41.1	17.6 ± 14.6	1.94 - 53.6
Local infested forest	ha	0.13 ± 0.20	0 – 0.65	0.24 ± 0.27	0 – 0.8	0.15 ± 0.14	0 – 0.42
Regional area conserved	ha	4.06 ± 5.32	0 - 16.3	9.58 ± 7.79	1.12 - 25.6	88.7 ± 55.6	29.6 - 204

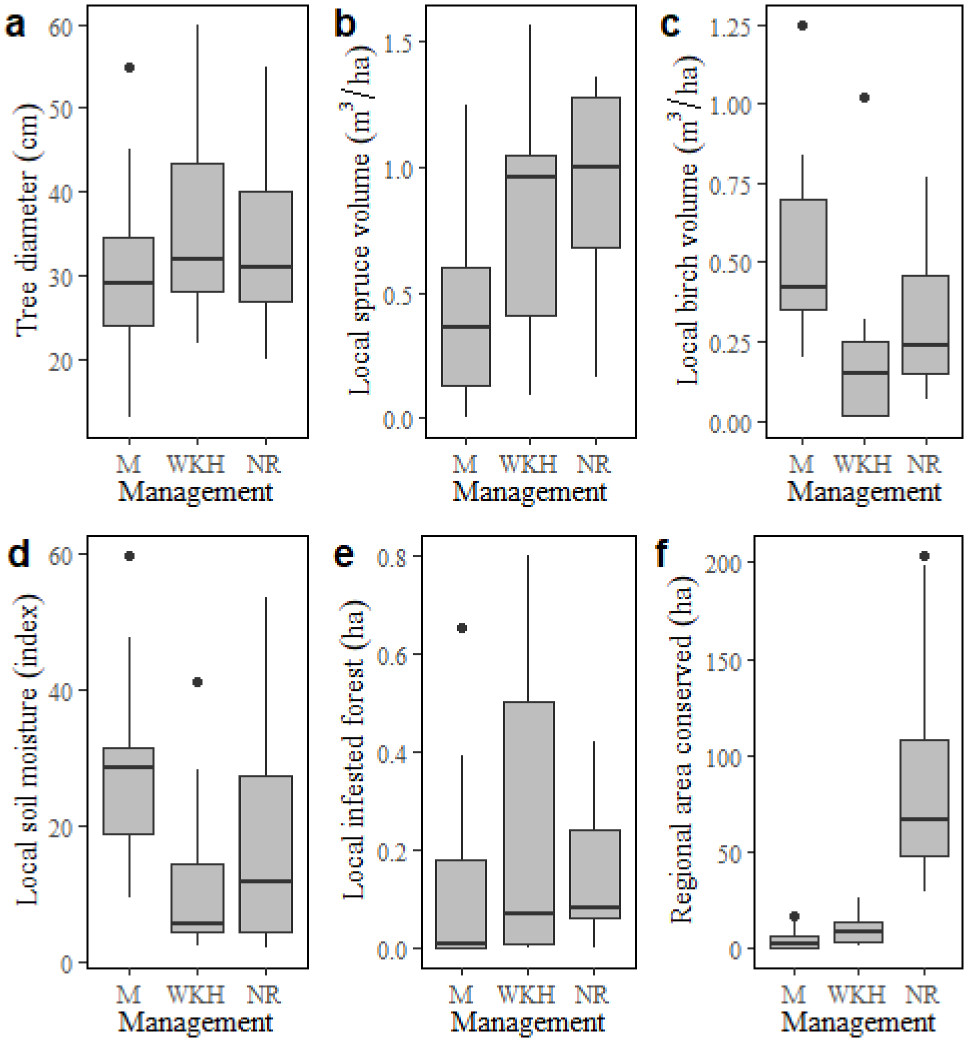
Appendix 2

Outputs of tests and multiple comparisons of spruce tree diameter, and landscape variables between managements. M = managed forests, WKH = woodland key-habitats, NR = nature reserves. The p-values are adjusted for multiple tests. For units, means ± SD, and ranges of variable see Appendix 1.

Variable	Estimate	SE	p-value
Tree diameter			
WKH - M	0.17218	0.04827	**<0.001**
NR - M	0.1299	0.04867	**0.008**
NR - WKH	-0.04228	0.05089	0.406
Local spruce volume			
WKH - M	0.90883	0.16666	**<0.001**
NR - M	0.98857	0.15689	**<0.001**
NR - WKH	0.07975	0.16809	0.635
Local birch volume			
WKH - M	-1.243	0.1321	**<0.001**
NR - M	-0.4907	0.1306	**<0.001**
NR - WKH	0.7523	0.1458	**<0.001**
Local infested forest			
WKH - M	1.15087	0.23889	**<0.001**
NR - M	1.18422	0.24913	**<0.001**
NR - WKH	0.03334	0.24788	0.893
Regional area conserved			
WKH - M	0.899	0.161	**<0.001**
NR - M	3.3672	0.1635	**<0.001**
NR - WKH	2.4682	0.1533	**<0.001**
Variable	z-value	-	p-value
Local soil moisture			
WKH - M	-5.88	-	**<0.001**
NR - M	-4.20	-	**<0.001**
NR - WKH	1.58	-	0.344

Appendix 3

Boxplots of the spruce tree diameter, and the local (within 100 m radius) and regional (within 1000 m radius) landscape variables in each management, M = managed forests, WKH = woodland key-habitats, NR = nature reserves. The boxplots show (a) tree diameter, (b) local spruce volume, (c) local birch volume, (d) local soil moisture, (e) local infested forest, and (f) regional area conserved. Bar: median; box: interquartile range (IQR); whiskers: min/max. values < 1.5 × IQR below/above box; dots: outliers.



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