



Abstract

A review by Cadotte et al. (2011) argue for the importance of using a functional diversity approach in conservation of ecosystem processes. In this study I focused on the functional group of cavity nesting bees, which are solitary bees creating their nests in above-ground cavities. I investigated how resources in a human altered landscape, in this case power line strips, may affect the abundance and species richness of the cavity nesting bees and two functional subgroups within the cavity nesting bees. Power line strips may function as habitat for cavity nesting bees by providing floral resources and possible nest sites. Brambles in power line strips may directly function as nest sites for the subgroup of excavator bees. Abandoned beetle holes in the dead wood found in the power line strips may function as nest sites for the subgroup of renter bees. Bees and beetles were sampled in power line strips at 27 different sites in the southeast Norway. I used regression analysis (generalized linear model (GLM)) to find which environmental variables best explained the abundance and species richness of cavity nesting bees, excavator bees and renter bees. The results showed that the abundance and species richness of cavity nesting bees, excavator bees and renter bees were positively associated with, and best explained by, the abundance of wood boring beetles. This implies that nest sites is the main limiting resource in power line strips, and that wood boring beetles, acting as an ecosystem engineer, are important in providing this nest sites. The abundance and species richness of renter bees are more positively related to the abundance of wood boring beetles when there are no brambles at the site. This indicate that the excavator bees and renter bees compete for nest sites in abandoned beetle holes when there are no brambles at the site. Management to conserve cavity nesting bees have to target and facilitate the abundance of wood boring beetles. This study stresses the importance of knowing the biology and indirect species interactions of the species in concern to prevent negative cascading effects.

Table of contents

1. Introduction.....	3
2. Materials and methods	6
2.1. Study area	6
2.2. Study species	6
2.3. Environmental variables.	10
2.4. Data analysis.....	12
3. Results	15
3.1. Availability of nest site resources.....	16
3.2. Availability of floral resources	30
4. Discussion.....	32
5. Acknowledgements.....	36
6. References.....	37
7. Appendix	

1. Introduction

A review by Cadotte et al. (2011) argue for the importance of using a functional diversity approach, and not only general species richness, in conservation of ecosystem processes. The definition of functional diversity is somewhat fuzzy (Petchey & Gaston 2006). Diaz and Cabido (2001) divide functional diversity into functional richness (i.e., number of functional traits present in a community) and functional composition (i.e., which functional traits are present in a community) and define functional traits as “the characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning” (Diaz and Cabido 2001 p. 654). Petchey & Gaston (2006) argued that one approach is to group species into functional groups based on their functional traits. The functional groups may further be divided into new functional subgroups based on other functional traits, and so on down to the level of interest (Petchey & Gaston 2006). The diversity in functional groups of pollinators may be positively associated with seed production (Hoehn et al. 2008) plant species richness and ecosystem sustainability (Fontaine et al. 2006). In this study I will focus on the functional group of pollinating bees and investigate how human caused land change may affect abundance and species richness within certain functional subgroups.

There are registered just above 20.000 species of bees in the world (Ruggiero 2009). Bees provide important ecosystem services for humans by pollinating wild plants and agricultural crops (Daily 1997). Ecosystem services are defined by Daily (1997 p. 3) as “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life”. Although the domestic honey bees (*Apis mellifera*) are often referred to as the most important pollinator economically (Watanabe 1994), the wild bees do contribute substantially to the pollination of agricultural products. For instance, Greenleaf and Kremen (2006) showed that the presence of wild bees could enhance honey bee pollination. Research done by Winfree et al. (2007) showed that wild bees may, to a great extent, compensate for the honey bees in pollinating intensively managed watermelon fields. (Winfree et al. 2007) argued that the wild bees are especially important because domestic bee populations are in decline in several parts of the world. However, in many countries, also the wild bees are in decline, mostly because of human activity (Michener 2007). Especially specialized bee species have shown a relative decline in the Netherlands and Britain since 1980 (Biesmeijer et al. 2006).

According to Westrich (1996), in order to function as a habitat for non-parasitic bees, an area must contain three key resources. Firstly, the site has to contain suitable nest sites. For example bare soil and sand, or different types of cavities and stems with soft inner pits, depending on nesting strategy. Secondly the site has to provide nesting materials. Third, the bees need floral resources like nectar, pollen and for some species floral oil. Which resources are used by the bees depends on the different bee species and, in the case of the opportunistic bee species, which resources are available. There has been much focus on the importance of floral resources determining the bee community composition and abundance, and less focus on the importance of nest sites and nesting materials (Roulston & Goodell 2011). However the availability of nesting resources do, to some degree, determine bee community structure (Potts et al. 2005) and may be positively associated with the bee species richness (Grundel et al. 2010) and bee abundance (Steffan-Dewenter & Schiele 2008). Steffan-Dewenter & Schiele (2008) even suggested that the nest sites are limited resource affecting the local population size of *Osmia rufa*. There are other studies that indicate that nest sites are limiting resources for bees. Danks (1971) suggested that the availability of nest sites limits the full reproductive potential for stem nesting solitary wasps and bees (Aculeate hymenoptera), and a study by Budrienè et al. (2004) found indications on inter-specific competition and niche differentiation for suitable nest sites among cavity nesting bees.

Power line strips are regularly managed to prevent tall trees to interrupt the electric power lines. This management ensure early succession vegetation that may function as source habitat for earlysuccession dependent species like shrubland birds (Askins et al. 2012) or provide alternative habitat for species dependent on semi-natural pastures (Berg et al. 2011). According to Michener (2007) many bee species prefer open habitats like moderately disturbed areas and forest edges.

Power line strips fits Michener (2007) description of a typical bee habitat with open areas, moderately disturbed by humans cutting down the trees, and the narrow shape of the power line strip that create edge habitats to the surrounding area. Russell et al. (2005) argued that power line strips provide potential stable habitat for bees and that power line strips may provide floral and nesting resources. The power line strips in an otherwise forested landscape may be have resemble clear cuts in forest. Romey et al. (2007) compared different intensity of logging on the diversity, species richness and abundance of wild bees in a northern hardwood forest in USA. Their results showed that the logging was associated with an increase in diversity, species

richness and abundance of the bees. Romey et al. (2007) suggested that the removal of trees gave light for more floral resources and the dead wood and weeds provided suitable nest sites for the bees.

In this study I divide the functional group of pollinating bees into cavity nesting bees and below ground nesting bees. The cavity nesting bees are solitary bees which place their nests in above-ground cavities. Solitary bees are bees where the females are alone in making nests and providing for her offspring (Michener (2007)). The below ground nesting bees, in contrast to the cavity nesting bees, place their nests in soil or sand underneath the ground surface (see Williams et al.(2010)). Some cavity nesting bees are specifically known to use bramble stems, rotten wood or abandoned beetle holes in wood as nest sites (Westrich 1989), resources which are readily found in power line strips (personal experience). The dead wood in the power line strips may attract wood boring insects like the wood boring beetles. The wood boring beetles are beetles where the larvae develop and pupate inside the wood, often in dead wood, and bore exit holes when leaving the tree trunk as imago (Ehnström & Axelsson 2002).

There are three main hypotheses in this study: Firstly, floral resources and nesting resources (i.e., specified as nest sites), are limiting resources affecting the abundance and species richness of cavity nesting bees in power line strips. Secondly, wood boring beetles and brambles are important in providing nest sites for these cavity nesting bees. Thirdly, there are two functional groups of cavity nesting bees based on their nest site biology. The first group, the excavator bees, are limited by the availability of nest sites in brambles. The second group, the renter bees, are limited by the availability of nest sites in abandoned insect holes in dead wood.

My predictions are:

- An increase in abundance and species richness of cavity nesting bees will be associated with an increase in presence of brambles (raspberries *Rubus idaeus* and species of blackberries *Rubus* spp), abundance of wood boring beetles, amount of dead wood and cover of floral resources.
- An increase in abundance and species richness of excavator bees will be associated with an increase in cover of brambles and the cover of floral resources, and less associated

with an increase in abundance of wood boring beetles.

- An increase in abundance and species richness of renter bees will be associated with an increase in abundance of wood boring beetles, amount of dead wood, and cover of floral resources, and less associated with an increase in cover of brambles.

2. Materials and methods

2.1. Study area

The study sites are scattered over approximately 40,000 km² area in south-East part of Norway. The area consist mostly by forests and bare mountainous areas. The forests are coniferous forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)(Skogoglandskap 2014). There is a gradient from the warm coastal areas in the south to a colder mountainous inland area in the north. The data presented in this theses, is a part of an ongoing study on how power-line strips impact on biodiversity. Candidate study sites were previously identified by distributing 84 sites evenly on a general map of the Statnett SF power line grid in southeast Norway. Thereafter, 51 of the 84 sites were selected by drawing lots. All the selected sites were located in power line strips with at least 200 m of forest on both sides. There were at least 9 km distance from the nearest site, which is further than the foraging range of most bees (Gathmann & Tscharrntke 2002). In 2009-2010 data on vegetation composition and abiotic factors were collected at all the sites. Among these 51 sites, 20 sites were haphazardly selected for data collection on insect fauna by use of flight interception traps in 2010 (10 sites), 2011 (10 sites) and 2013 (10 sites).

2.2. Study species

Bees

The main study species are the solitary cavity nesting Megachilid and Hylaeinae bees (see also (Williams et al. 2010)). In this study, most of the cavity nesting bees were assigned to either of

two main groups of bees, based on their nesting biology. The first main group is **the renter bees**, which may use suitable pre-existing cavities as nest sites. The renter bees may use abandoned insect holes in dead wood as nest sites. The second main group of bees is **the excavator bees**, which are able to excavate their own nesting holes in old bramble stems. I define brambles as species of *Rubus spp*, like raspberries and blackberries, which have ligneous stems with a soft inner core. The bees are either obligate excavator bees and obligate renter bees (i.e., the bees species is either a renter or an excavator), or they may be facultative excavator and renter bees (i.e., the bees species is both an renter and excavator bee). A few of the cavity nesting bees did not fit any of the main groups, and were categorized as cavity nesting bees.

Bee collection

Flying insects were sampled using flight-interception traps allowing for a standardized sampling protocol over a large geographical area with little or no bias due to collector experience. The flight interception traps consisted of two rectangular plates of transparent plexiglass (polymethylmetacrylate) each measuring 370 x 210 mm (Fig.1). The plexiglass plates were assembled so that they formed a vertical cross which was placed vertically on the wide end of a plastic funnel. The funnel lead to a bottle of preservation liquid (a 1:1 mix of propylenglycole and water) and a drop of detergent brand Zalo, (Lilleborg, Norway) to break the surface tension. Small holes were drilled above the water line of the bottles to ensure drainage of surplus rainwater. The traps were deployed in late April or in the beginning of May, and trapping was carried out continuously until the traps were demounted in August. The bottles with insects in preservation liquid were collected and replaced with new ones four times (approximately once a month) during the field season.



Figure 1. Flight interception trap. Photot aken by Lise Davanger Häusler, summer 2003.

Four flight interception traps were placed in the 10 sites sampled in 2009 and 2010. I added an extra trap when conducting the survey in 2013 to avoid the loss of information from an entire study site in the case a trap had been damaged. In each site flight interception traps were deployed in the middle of each strip center plot (Fig. 2). A random number generator (www.random.org) was used to select one out of the five traps which was then removed from each of the 10 sites sampled in 2013. All of the 30 sites thereby potentially provided insects from four traps. Three sites from the collection of 20 sites from 2009 and 2010 were discarded before data processing since they had lost >1 trap during one of the four sampling periods. Two of the remaining sites had lost one trap during sampling period 1 and 4. To ensure equal sampling effort from each site, the random number generator (www.random.org) was used to randomly select and remove the data collected from one trap during the first and fourth sampling period from all sites.

In the lab the contents of each bottle of insects was sieved through a fine-meshed net (plankton net). Thereafter the insects were rinsed with water and then transferred to marked glass

containers filled with 80% ethanol and 20% water. The collected bees were washed in 80% ethanol and blow-dried before pinning. The Bees were identified to species by Markus Sydenham by the use of regional identification keys (AMIET et al. 1999; AMIET 2004). He also categorized the bees into cavity nesting bees, excavator bees and renter bees following Westrich (1989). The collected beetles were identified by Sindre Ligaard (national expert in beetle taxonomy) according to the species identification key by Silfverberg (2004). He also noted which of the beetles that may create holes into wood according to (*Fauna entomologica Scandinavica* ; Freude et al. 1964; Landin 1957; Nationalnyckeln till Sveriges flora och fauna ; Palm 1959; Rennerfelt 1951). The nomenclature used in this study follow The Norwegian Biodiversity Information Centre (accessed January 2014).

I quantified the number of individuals (abundance) and number of species (species richness) within each of the following three groups: all cavity nesting bees, excavator bees, and renter bees. Thus, I had six different response variables: (1) Abundance of cavity nesting bees, (2) Species richness of cavity nesting bees, (3) Abundance of excavator bees, (4) Species richness of excavator bees, (5) Abundance of renter bees and (6) Species richness of renter bees.

Only beetles producing exit holes large enough for at least the smallest of the collected bees were included. I used information from studies documenting the average diameter of trap-nests utilized by cavity nesting bees (Budrienè et al. 2004; Gathmann et al. 1994). For species where this information could not be found, the inter-tegular distances (ITD) were measured and compared to the ITD of the species with published information on nest site diameters. The smallest bee species had an inter-tegular distance of approximately 0.9 mm and constructed nests in trap nests with an average diameter of 2.95 mm. I therefore only included beetles producing exit wholes with a diameter of at least approximately 3 mm. The biggest of the renter bees had an inter-tegular diameter of 3.3 mm and the average trap nesting diameter of 7.5 mm. I set the maximum exit hole diameter to be approximately 8 mm. I used Ehnström and Axelsson, (2002) to find the approximate diameter of the beetle exit holes. When there was no exit hole diameter present in the literature, we used the exit hole diameter for close related and equally sized beetles.

2.3. Environmental variables.

Based on the beetles caught by the flight interception traps, I quantified the total number of wood boring beetles (Abundance of wood boring beetles) and the number of species of wood boring beetles (species richness of wood boring beetles) for each site. I also calculated the odds measure of diversity (OD) for beetles. The odds measure of diversity (OD) is defined by Kvalseth (1991, p. 124) as “the odds that two individuals elected at random (with replacement) from the sample are of different species.”

Environmental variables were surveyed in each site in 12 rectangular plots measuring 4 x 5 meters. The plots were placed in 3 groups of four plots running perpendicularly with the power line strips. One group of plots was placed in the center of the power line strips (S = Strip center in Fig. 2). Another group was situated in the power-line strip running along the forest edge (Se = strip edge in Fig. 2). The third group was placed within the forest edge parallel to the strip edge plots (Fe = forest edge in Fig. 2). The distance between the two nearest plots in a group was 50 meters. Each plot contained five 1x1 meter subplots along the center line of the plot, in which plant and dead wood cover registrations were carried out (see below).

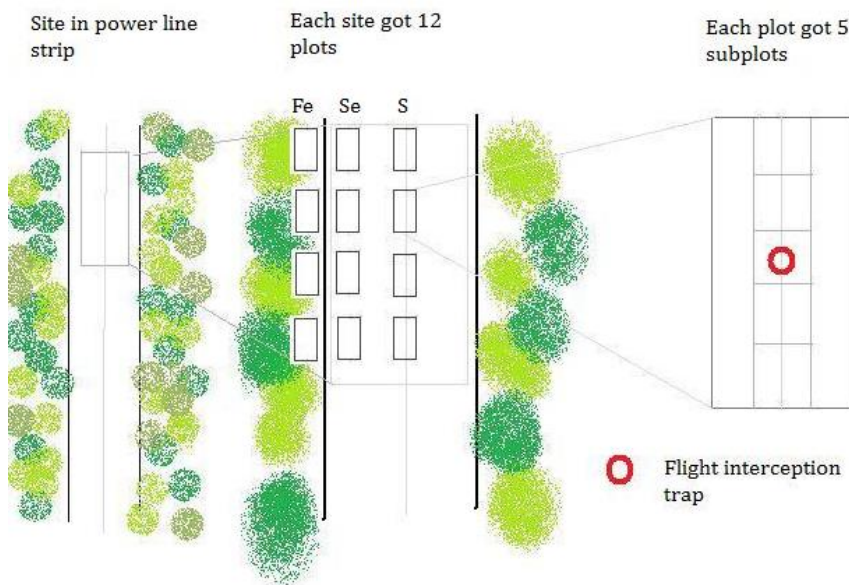


Figure 2. A schematic overview of one of the 27 sites in this study. S = Strip center, Se = strip edge, Fe = forest edge.

The percentage cover of all annual and perennial herbaceous flowering plant species was assessed by visual estimation in all the subplots in the strip center (S) and strip edge (Se).

I divided the floral resources into three groups: Group 1 consists of only plant species of the Asteraceae family. Group 2 consist of plant species of the Fabaceae, Plantaginaceae and Lamiaceae families. Group 3 consist of all the species from both group 1 and group 2. For each group, I calculated the total per cent cover for each of the subplots. Then I calculated the average cover for the subplots and used this as an estimate of the plant cover for the whole plot. The average of the estimated plant cover for the plots was used to estimate the plant cover for the whole site. The cover of Asteraceae ranged from 0 to 1%, and the cover of Plantaginaceae and Lamiaceae ranged from 0 to 10%. The total cover of Asteraceae, Fabaceae, Plantaginaceae and Lamiaceae ranged from 0 to 10 %

I also estimated the percentage cover of brambles (in this case *Rubus idaeus* and *Rubus fruticosus*) in the same subplots. I calculated the average cover for the subplots and used this as an estimate of the plant cover for the whole plot. The average of the estimated plant cover for the plots was used to estimate the plant cover for the whole site. The percentage of brambles ranged from approximately 0% to 1.5%.

The amount of dead wood in each site was estimated in three different ways. First, the estimate of standing dead wood was based on a count of all standing dead trees in all plots (S, Se and Fe) for each site (Fig. 2). The average number of standing dead trees of the plots was calculated as an estimate for the amount of standing dead wood for the whole site. The average number of standing dead wood ranged from 0 to 2. Second, the same method as for standing dead wood was used to estimate the amount of logs. Only logs with a diameter greater than 3 centimeter at the thickest part of the tree trunk, was counted. The average number of logs ranged from 0 to 13. Third, the percentage cover of dead wood was determined by visual estimation in each subplot in the S, Se, and Fe-plots. I used the average of the per cent cover of dead wood in the subplot to estimate the dead wood cover for the whole plot. The cover of dead wood in each site was estimated by calculating the average of the estimated dead wood cover for the plots in the site.

The per cent cover of dead wood ranged from approximately 0 to 9.6%.

Digital maps (AR5^{©geovekst}) provided by the Norwegian Forest and Landscape Institute (Bjørndal & Bjørkelo 2006) were used to extract GIS information on landscape context within a 2000 m radius. The digital maps were the most accurate maps available in Norway at the time the study was conducted. The maps were used to find the forest productivity class (graded to low, medium, high or no productivity) for each plot. The forest productivity classes in the plots were graded: no productivity = 0, low productivity = 1, medium productivity = 2 and high productivity = 3. The forest productivity index for the sites was estimated as the average value of the productivity class in the sites. The forest productivity index ranged from 0.35 to 3. ArcGIS (ESRI, CA, USA) was used to extract the percentage cover of forests within the radius of 1000 meters from the sites. The percentage forest cover ranged from 38 to 97 % for the 27 sites.

Altitude has been shown to be an important factor in structuring wild bee communities (Hoiss et al. 2012). I therefore also measured the Altitude of each plot by the use of a hand held GPS. The average altitude of the plots was used as an estimate for the site altitude. The altitude ranged from 32 to 560 meter above sea level.

2.4. Data analysis

The data analyses were carried out using R version 2.15.1. (R Core Team 2012)

Firstly I carried out exploratory analyses, following the recommendations in Zuur et al. (2010). I used boxplots and Cleveland dotplots to check for any unusual observations and indications of heterogeneity. Several of the explanatory variables had a highly skewed distribution with many zeroes and low values and a few observations with high values.

Because the bramble data and the Asteraceae data were particularly skewed, I converted them into categorical values with two levels: Absence and presence.

I looked for collinearity between the explanatory variables and possible relationships between explanatory variables and response variables, by use of a correlogram (Wright 2013) (Appendix 1).

If the correlation coefficient from a correlation analysis between a pair of explanatory variables exceeded 0.5, the two explanatory variables were treated in separate statistical models.

Based on the exploratory analyses, I decided to include all the sites in the statistical analyses presented in this thesis, although one site had somewhat divergent values for the response variables. When I excluded this site from the statistical analyses, the results of the analyses were not qualitatively different, but the relationships between the response and the explanatory variables were slightly stronger.

All the response variables were significantly correlated with each other with Pearson's correlation coefficients (r) ranging from 0.63 to 0.93 (Appendix 1). For the explanatory variables, there was a positive correlation between the presence of Asteraceae plants vs the overall plant cover of *Fabaceae*, *Plantaginaceae* and *Lamiaceae* families ($r = 0.41$), and between the abundance of wood boring beetles vs altitude ($r = 0.44$). I dropped the explanatory variable "forest productivity index" because it correlated with the presence /absence of Asteraceae plants ($r = 0.52$) and the estimated cover of plant species of the *Fabaceae*, *Plantaginaceae* and *Lamiaceae* families ($r = 0.55$). I also dropped the explanatory variables "percentage cover of dead wood" and the total cover of Asteraceae, *Fabaceae*, *Plantaginaceae* and *Lamiaceae* plants because they correlated with explanatory variables.

Statistical modelling

For each response variable I fitted a generalized linear model (GLM) with log link function and Poisson or negative binomial distribution which is appropriate for count data (see Zuur et al. (2009). If graphical diagnostics and the generalized Pearson statistic (Crawley 2013) showed that the Poisson regression model was over-dispersed, i.e., had a p -value substantially larger than 1, I re-fitted the model using negative binomial distribution (Venables & Ripley 2002), and model adequacy was confirmed by graphical validation. The level of significance was 0.05.

I created models for each of the six response variables: Abundance of cavity nesting bees, abundance of excavator bees, abundance of renter bees, species richness of cavity nesting bees,

species richness of excavator bees and species richness of renter bees. The availability of nesting resources and the floral resources were analysed separately with different models. I included the species richness of wood boring beetles in the models with abundance of wood boring beetles to see if the species richness significantly contributed to the model. I did the same with the final models for the floral resources: adding the floral resources in the final models for the availability of nest sites, to see if the floral resources contributed significantly to the models.

When building a model for the availability of nesting resources (i.e., using beetles as proxy for nesting resources), tree of the main explanatory variables were correlated (correlation coefficient > 0.5). Therefore, for each of the 6 bee response variables, I ran separate models for the abundance of wood boring beetles, the species richness of wood boring beetles and the odds measure of diversity (OD) for the wood boring beetles. In addition, the other explanatory variables were included as covariates in each of these three separate models in the model building process.

For each of the models created, I performed a pre-selection of variables by first fitting individual models for all the explanatory variables, and then including only variables with $p \leq 0.10$ in single-variable models in the full model. For each response variable, explanatory variables were retained in the final model through backward elimination (Crawley 2013) if their influence on the response was statistically significant ($p \leq 0.05$).

For all the models of nesting resources availability I tested for interactions between: the abundance of wood boring beetles and the presence of brambles, abundance of wood boring beetles and the estimates of dead wood, species richness of wood boring beetles and brambles, and the species richness of wood boring beetles and the estimates for dead wood.

I log-transformed the explanatory variables of the residuals from the final models were not normal distributed.

The pseudo R^2 were taken from Zuur et al. (2009, p. 211): $100 * ((\text{Null deviance} - \text{Residual deviance}) / \text{Null deviance})$

3. Results

In total 147 individuals of solitary were sampled and identified to 15 species. (Table 1) The largest group of bees was the obligate excavator bees with 111 individuals and 4 species. This group comprised approximately 75% of the solitary bees sampled. The second largest group was the facultative excavator and renter bees with 18 individuals and 5 species. The obligate renter bees had 16 individuals and 5 species, and there were only two individuals and 1 species of other cavity nesting bees (Table 1). All the cavity nesting bee species found in this study belong to the genera *Hoplitis*, *Megachile* and *Osmia* of the Megachilidae family, and the genus *Hylaeus* of the Colletidae family.

In total 835 individuals and 24 species of wood boring beetles were sampled (Table 2). Approximately 90 % of the beetle individuals belonged to the family Cerambycidae. The beetle exit hole diameter ranged from 3 mm to 8 mm. Approximately 41% of the species and approximately 27% of the total abundance of the wood boring beetles sampled create exit holes with a diameter greater than 4 mm.

Table 1. Cavity nesting bees recorded with flight interception traps placed in power line strips at 27 different sites in the southeast part of Norway. The nesting biology and the number of individuals captured are shown. The renters are obligate renter bees that only use abandoned insect holes as nest sites. Excavators are obligate excavator bees that only use self-made nesting holes in brambles. The renters + excavators are both renters and excavators. The other cavity nesting bee species, *Megachile nigriventris* is known to excavate nest holes in soft dead wood (Westrich 1989)

Family	Species	Nesting biology	Individuals	Mean	SD
Colletidae	<i>Hylaeus angustatus</i>	Renter + Excavator	7	0,50	1,4
Colletidae	<i>Hylaeus annulatus</i>	Excavator	17	1,2	3,2
Colletidae	<i>Hylaeus brevicornis</i>	Renter + Excavator	2	0,14	0,45
Colletidae	<i>Hylaeus communis</i>	Excavator	24	1,7	4,7
Colletidae	<i>Hylaeus confusus</i>	Excavator	69	4,9	13
Colletidae	<i>Hylaeus hyalinatus</i>	Renter + Excavator	7	0,50	1,5
Colletidae	<i>Hylaeus rinki</i>	Excavator	1	0,071	0,26
Megachilidae	<i>Hoplitis tuberculata</i>	Renter	1	0,071	0,26
Megachilidae	<i>Megachile nigriventris</i>	Other cavity nesting bee	2	0,14	0,45
Megachilidae	<i>Megachile versicolor</i>	Renter + Excavator	1	0,071	0,26
Megachilidae	<i>Osmia bicornis</i>	Renter	1	0,071	0,26
Megachilidae	<i>Osmia caerulescens</i>	Renter + Excavator	1	0,071	0,26
Megachilidae	<i>Osmia nigriventris</i>	Renter	8	0,57	1,6
Megachilidae	<i>Osmia parietina</i>	Renter	4	0,29	0,81
Megachilidae	<i>Osmia uncinata</i>	Renter	2	0,14	0,45

Table 2. Wood boring beetles (beetle species that are known to bore holes with a diameter greater than 3 mm in dead wood) recorded with flight interception traps placed in power line strips at 27 different sites in southeast Norway.

Family	Species	Individuals	Mean	SD
Anthribidae	<i>Platystomus albinus</i>	3	0,11	0,42
Buprestidae	<i>Anthaxia quadripunctata</i>	38	1,41	3,0
Buprestidae	<i>Anthaxia similis</i>	3	0,11	0,42
Buprestidae	<i>Buprestis octoguttata</i>	19	0,70	1,9
Cerambycidae	<i>Aegomorphus clavipes</i>	1	0,037	0,19
Cerambycidae	<i>Alosterna tabacicolor</i>	1	0,037	0,19
Cerambycidae	<i>Anoplodera maculicornis</i>	101	3,7	4,3
Cerambycidae	<i>Anoplodera rubra</i>	100	3,7	5,6
Cerambycidae	<i>Anoplodera sanguinolenta</i>	81	3,0	4,4
Cerambycidae	<i>Arhopalus rusticus</i>	1	0,037	0,19
Cerambycidae	<i>Clytus arietis</i>	15	0,56	1,0
Cerambycidae	<i>Gaurotes virginea</i>	2	0,074	0,38
Cerambycidae	<i>Leptura maculata</i>	1	0,037	0,19
Cerambycidae	<i>Lleptura melanura</i>	351	13,00	12
Cerambycidae	<i>Lleptura nigra</i>	1	0,037	0,19
Cerambycidae	<i>Leptura quadrifasciata</i>	70	2,6	3,0
Cerambycidae	<i>Pogonocherus fasciculatus</i>	2	0,074	0,27
Cerambycidae	<i>Rhagium inquisitor</i>	18	0,67	1,0
Cerambycidae	<i>Rhagium mordax</i>	18	0,67	1,0
Cerambycidae	<i>Saperda scalaris</i>	1	0,037	0,19
Cerambycidae	<i>Tetropium castaneum</i>	2	0,074	0,27
Curculionidae	<i>Dendroctonus micans</i>	1	0,037	0,19
Curculionidae	<i>Pissodes pini</i>	2	0,074	0,38
Elateridae	<i>Anostirus castaneus</i>	3	0,11	0,32

3.1. Availability of nest site resources

All the six bee response variables (i.e., abundance of cavity nesting bees, species richness of cavity nesting bees, abundance of excavator bees, species richness of excavator bees, abundance of renter bees and species richness of renter bees) were positively related to the abundance of wood boring beetles. Furthermore, no other explanatory variables were significant when included as a covariate in the models together with in the abundance of wood boring beetles, even though they were significantly related to the response variables when included as the only explanatory variable.

All the six bee response variables were also positively related to the species richness of wood boring beetles. For the models explaining the abundance of cavity nesting, excavator and renter

bees, the presence of brambles was the only covariate that significantly contributed to the models together with the species richness of wood boring beetles. For the models explaining species richness of cavity nesting, excavator and renter bees, no other explanatory variables were significant when included as a covariate in the models together with the species richness of wood boring beetles, even though they were significantly related to the response variables when included as the only explanatory variable. The pseudo R^2 was invariably greater for the models with abundance of wood boring beetles as explanatory variable compared to the models with species richness of wood boring beetles (sometimes together with presence of brambles) as explanatory variables.

3.1.1. Cavity nesting bees

The abundance of cavity nesting bees was positively related to the abundance of wood boring beetles. The abundance of bees increased exponentially with increasing number of beetle individuals (Table 3, Fig. 3). The abundance of wood boring beetles explained 54% of the variation in the abundance of cavity nesting bees. One site was identified as a potential outlier (Fig. 3) However, refitting the model without this site did not qualitatively change the results, but provided a better fit (pseudo $R^2 = 0.75$).

The abundance of cavity nesting bees was also positively related to the species richness of wood boring beetles and the presence of brambles (Table 3). Sites with brambles were likely to have a higher abundance of cavity nesting bees compared to sites with the same species richness of wood boring beetles but without the brambles. The species richness of wood boring beetles and the presence of brambles explained 34% of the variation in the abundance of cavity nesting bees. This was less explained variation compared to the above mentioned model where the abundance of cavity nesting bees was explained by the abundance of wood boring beetles (pseudo $R^2 = 54$).

Table 3. The relationship between the abundance of cavity nesting bees (solitary bees that make their nests in above ground cavities) and the presence of brambles (raspberries and blackberries) and the species richness and abundance of wood boring beetles (beetles that bore holes with a diameter ≥ 3 mm in dead wood). The abundance and species richness of wood boring beetles were correlated ($r = 0.50$) and therefore treated in separate models.

Response variable	Explanatory variables	β	SE	d.f.	z	P	Pseudo- R^2
<i>Abundance of cavity nesting bees</i>							0.54
	Intercept	0.61	0.22	1	2.8	0.010	
	Abundance of wood boring beetles	0.027	0.0047	1	5.7	< 0.0001	
<i>Abundance of cavity nesting bees</i>							0.34
	Intercept	-0.36	0.52	1	-0.68	0.49	
	Species richness of wood boring beetles	0.25	0.070	1	3.5	<0.001	
	With brambles (vs no brambles)	0.76	0.32	1	2.3	0.019	

The models are generalized linear models (GLM) with negative binomial distribution and log link, $n = 27$. Other explanatory variables tested, but found not to be significant, are: Altitude (m), amount of forest in a diameter of 1000 meters from site (m^2), average number of standing dead trees per $20m^2$ plot, average number of logs per $20 m^2$ plot, and odds measure of diversity (OD) of wood boring beetles. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in the southeast Norway. (Fig.1)

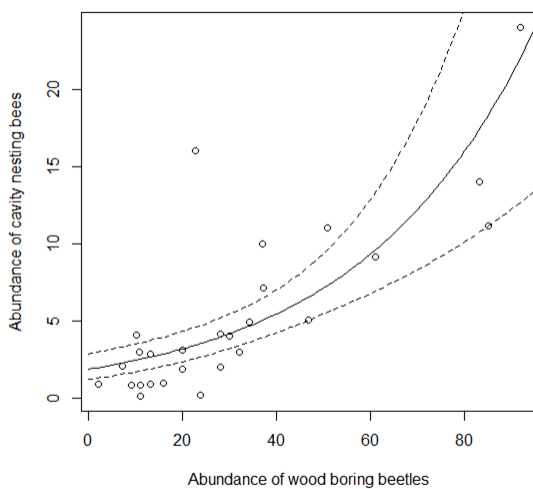


Figure 3. Abundance of cavity nesting bees (solitary bees known to make nests in above ground cavities) in relation to the abundance of wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 3.

The species richness of cavity nesting bees was positively related to the abundance of wood boring beetles. The species richness of bees increased exponentially with increasing number of beetle individuals (Table 3, Fig.4) The abundance of wood boring beetles explained 42% of the variation in the species richness of cavity nesting bees.

The species richness of cavity nesting bees was also positively related to the species richness of wood boring beetles. (Table 4, Fig.5). The species richness of wood boring beetles explained 34% of the variation in species richness of cavity nesting bees. This is less explained variation compared to the above mentioned model where the species richness of cavity nesting bees was explained by the abundance of wood boring beetles.

Table 4. The relationship between the species richness of cavity nesting bees (solitary bees that place their nests in above ground cavities) and the species richness and abundance of wood boring beetles (beetles that bore holes with a diameter ≥ 3 mm in dead wood). The abundance and species richness of wood boring beetles were correlated ($r = 0.50$) and therefore treated in separate models.

Response variable	Explanatory variables	β	SE	d.f.	z	P	Pseudo - R^2
<i>Species richness of cavity nesting bees</i>							0.42
	Intercept	0.38	0.21	1	1.8	0.069	
	Abundance of wood boring beetles	0.020	0.0041	1	3.7	<0.001	
<i>Species richness of cavity nesting bees</i>							0.34
	Intercept	-0.14	0.39	1	-0.37	0.70	
	Species richness of wood boring beetles	0.17	0.050	1	3.1	<0.01	

The models are generalized linear models (GLM) with poisson distribution and log link, n = 27. Other explanatory variables tested, but found not to be significant, are: presence of brambles (raspberries and blackberries), altitude (m), amount of forest in a diameter of 1000 meters from site (m^2), average number of standing dead trees per 20 m^2 plot, average number logs per 20 m^2 plot, and odds measure of diversity (OD) of wood boring beetles. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in southeast part of Norway.

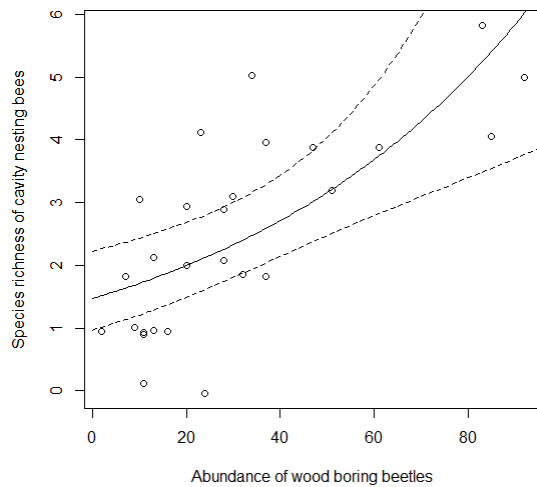


Figure 4 Species richness of cavity nesting bees (solitary bees known to place their nests in above ground cavities) in relation to the abundance of wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 4.

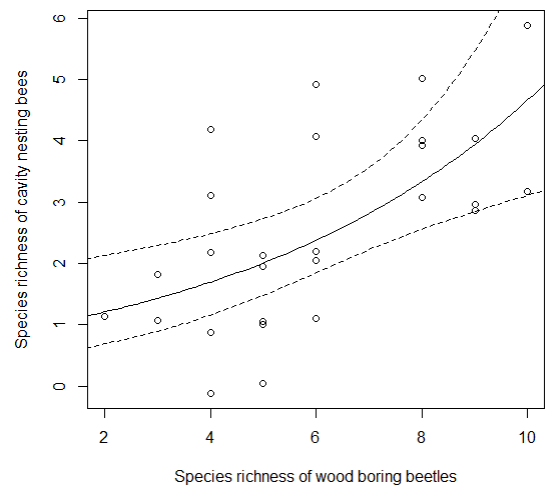


Figure 5 Species richness of cavity nesting bees (solitary bees known to place their nests in above ground cavities) in relation to the species richness of wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 4.

3.1.2. Excavator bees

The abundance of excavator bees was positively related to the abundance of wood boring beetles; the abundance of bees increased exponentially with increasing number of beetle individuals. (Table 5, Fig.6). The abundance of wood boring beetles explained 47% of the variation in the abundance of excavator bees. One site was identified as a potential outlier (Fig. 6). However, refitting the model without this site did not qualitatively change the results, but provided a better fit (pseudo $R^2 = 0.70$).

The abundance of excavator bees was also positively related to the species richness of wood boring beetles and the presence of brambles (Table 5). Sites with brambles were likely to have a higher abundance of excavator bees compared to sites with the same species richness of wood boring beetles but without the brambles. The species richness of wood boring beetles and presence of brambles explained 32% of the variation in abundance of excavator bees. This is less explained variation compared to the above mentioned model where the abundance of excavator bees was explained by the abundance of wood boring beetles (pseudo $R^2 = 47$).

Table 5. The relationship between the abundance of excavator bees (solitary bees that may excavate their own nesting holes in bramble stems) and the presence of brambles (raspberries and blackberries) and the species richness and abundance of wood boring beetles (beetles that bore holes with a diameter ≥ 3 mm in dead wood). The abundance and species richness of wood boring beetles were correlated ($r = 0.50$) and therefore treated in separate models.

Response variable	Explanatory variables	β	SE	d.f.	z	P	Pseudo- R^2
<i>Abundance of excavator bees</i>							0.47
	Intercept	0.49	0.25	1	2.0	0.049	
	Abundance of wood boring beetles	0.027	0.010	1	4.9	<0.0001	
<i>Abundance of excavator bees</i>							0.32
	Intercept	-0.56	0.56	1	-1.0	0.32	
	Species richness of wood boring beetles	0.26	0.080	1	3.4	<0.001	
	With brambles (vs no brambles)	0.77	0.34	1	2.2	0.03	

The models are generalized linear models (GLM) with negative binomial distribution and log link, $n = 27$. Other explanatory variables tested, but found not to be significant, are: Altitude (m), amount of forest in a diameter of 1000 meters from site (m^2), average number of standing dead trees per 20m² plot, average number of logs per 20m² plot, and odds measure of diversity (OD) of wood boring beetles. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in the south-eastern part of Norway.

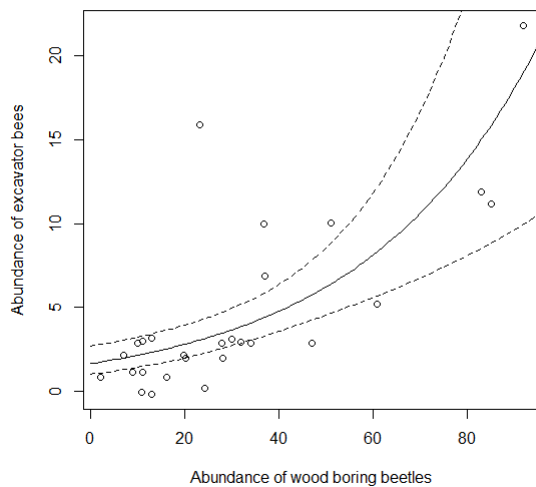


Figure 6 Abundance of excavator bees (solitary bees that are able to excavate nesting holes in bramble stems) in relation to the abundance of dead wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 5.

The species richness of excavator bees was positively related to the abundance of wood boring beetles. The species richness of bees increased exponentially with increasing number of beetle individuals (Table 6, Fig.7) The abundance of wood boring beetles explained 31% of the variation in species richness of excavator bees.

The species richness of excavator bees was also positively related to the species richness of wood boring beetles (Table 6, Fig.8). The species richness of wood bring beetles explained 29% of the variation in species richness of excavator bees. This is less explained variation compared to the above mentioned model where the species richness of excavator bees was explained by the abundance of wood boring beetles.

Table 6. The relationship between the species richness of excavator bees (solitary bees that may excavate their own nesting holes in bramble stems) and abundance and specie richness of wood boring beetles (beetles that bore holes with a diameter ≥ 3 mm in dead wood). The abundance and species richness of wood boring beetles were correlated ($r = 0.50$) and therefore treated in separate models.

Response variable	explanatory variables	β	SE	d.f.	z	P	Pseudo - R^2
<i>Species richness of excavator bees</i>							0.31
	Intercept	0.20	0.24	1	0.88	0.38	
	Abundance of wood boring beetles	0.010	0.0048	1	2.9	<0.01	
<i>Species richness of excavator bees</i>							0.29
	Intercept	-0.34	0.43	1	-0.77	0.44	
	Species richness of wood boring beetles	0.16	0.060	1	2.7	0.010	

The models are generalized linear models (GLM) with poisson distribution and log link, n = 27. Other explanatory variables tested, but found not to be significant, are: presence of brambles (raspberries and blackberries), altitude (m), amount of forest in a diameter of 1000 meters from site (m^2), average number of standing dead trees per 20 m^2 plot, average number of lying dead trees per 20 m^2 plot, and odds measure of diversity (OD) of wood boring beetles. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in southeast part of Norway.

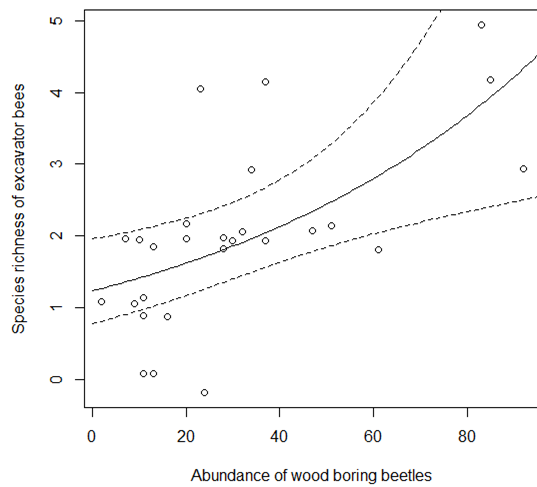


Figure 7 Species richness of excavator bees (solitary bees that may excavate their own nesting holes in bramble stems) in relation to the abundance of wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 6.

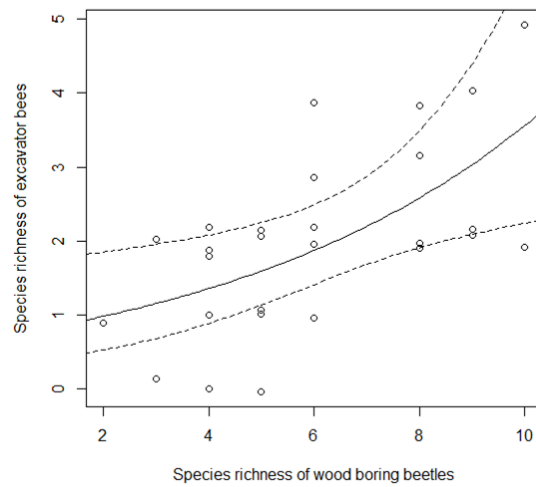


Figure 8 Species richness of excavator bees (solitary bees that may excavate their own nesting holes in bramble stems) in relation to the species richness wood boring beetles (of the beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 6.

3.1.3. Renter bees

The abundance of renter bees was positively related to the abundance of wood boring beetles. The abundance of bees increased exponentially with increasing number of beetle individuals (Table 7, Fig. 9). The abundance of wood boring beetles explained 55% of the variation in abundance of renter bees.

There was a possible interaction ($P = 0.067$) between the abundance of wood boring beetles and the brambles. The abundance of renter bees is more positively related to the abundance of wood boring beetles when there are no brambles at the sites, compared to when there are brambles at the sites (Table 7, Fig. 10). The interaction between the abundance of wood boring beetles and the presence of brambles explained 58% of the variation in abundance of renter bees. That is a higher explained variation compared to the above mentioned model where the brambles and the interaction between the abundance of wood boring beetles and the brambles were not included

The abundance of renter bees was also significant positively related to the species richness of the wood boring beetles and the presence of brambles (Table 7). There was a higher abundance of renter bees in sites with brambles compared to sites without brambles. The species richness of wood boring beetles and the presence of brambles explained 27% of the variation in the abundance of renter bees. This was a less explained variation compared to the two above mentioned models where the abundance of renter bees was explained by the abundance of wood boring beetles, with and without the interaction with brambles.

Table 7. The relationship between the abundance of reenter bees (solitary bees that may use abandoned insect holes as nest site) and the presence of brambles (raspberries and blackberries) and the species richness and abundance of wood boring beetles (beetles that bore holes with a diameter ≥ 3 mm in dead wood). The abundance and species richness of wood boring beetles were correlated ($r = 0.50$) and therefore treated in separate models.

Response variable	Explanatory variables	β	SE	d.f.	z	P	Pseudo - R^2
<i>Abundance of reenter bees</i>							0.55
	Intercept*	-4.5	1.0	1	-4.3	<0.0001	
	log(abundance of wood boring beetles)	1.4	0.27	1	5.0	<0.0001	
<i>Abundance of reenter bees</i>							0.58
	Intercept*	-2.5	0.93	1	-2.6	< 0.01	
	Abundance of dead wood boring beetles	0.078	0.026	1	3.0	<0.01	
	With brambles (vs no brambles)	1.6	1.0	1	1.5	0.14	
	Interaction bramble and abundance dead wood boring beetles ^a	-0.050	0.027	1	-1.8	0.067	
<i>Abundance of reenter bees</i>							0.27
	Intercept **	-2.1	0.80	1	-2.6	0.010	
	Species richness of wood boring beetles	0.25	0.10	1	2.5	0.013	
	With brambles (vs no brambles)	1.1	0.50	1	2.2	0.025	

* Generalized linear models (GLM) with poisson distribution and log link.

** Generalized linear models (GLM) with negative binomial distribution and log link.

a When dropped interaction (brambles x abundance wood boring beetles) the model becomes:

Intercept: $z = -3.0$, $P = <0.01$

Abundance of wood boring beetles: $z = 4.4$, $P = <0.0001$,

With brambles (vs no brambles) $z = -0.077$, $P = 0.94$, Pseudo- $R^2 = 0.52$

Other explanatory variables tested, but found not to be significant, are: Altitude (m), amount of forest in a diameter of 1000 meters from site (m^2), average number of standing dead trees per 20 m^2 plot, average number logs per 20 m^2 plot, and odds measure of diversity (OD) of wood boring beetles. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in the southeast part of Norway. $n = 27$.

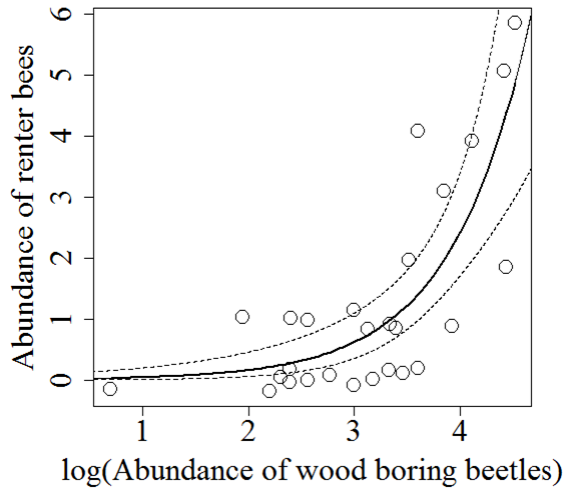


Figure 9. Abundance of renter bees (solitary bees that may use abandoned insect holes as nest sites) in relation to the log-e-transformed abundance of wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 7.

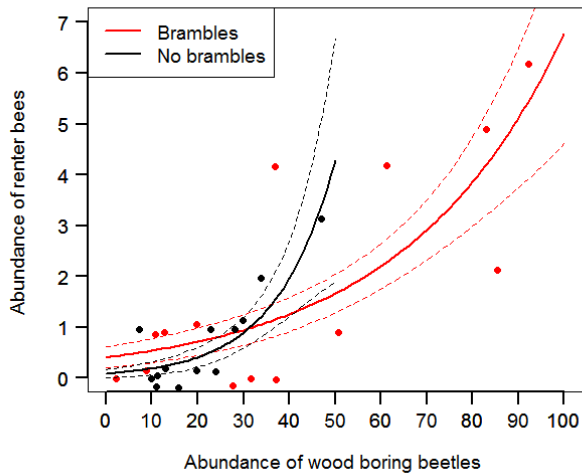


Figure 10 The abundance of renter bees (solitary bees using abandoned insect holes as nest site) were related differently to the abundance of wood boring beetles (beetles known to bore holes with a diameter greater than 3 mm in dead wood) depending on if there are brambles (red solid line) or no brambles (black solid line) at the site. The dotted lines mark the 95% confidence interval for the two models. The dots represent the observations, including some random noise (jitter) to separate similar observations. The red dots represent sites with brambles, and the black dots represent sites without brambles. The interaction between brambles and wood boring beetles got a p-value on 0.067. There are only sampled less than 50 wood boring beetles on sites without brambles, therefore the limited fitted values for the black line. For further details, see table 7.

The species richness of renter bees was positively related to the abundance of wood boring beetles. The Species richness of bees increased exponentially with increasing number of beetle individuals the abundance of wood boring beetles explained 40% of the variation in the species richness of renter bees.

There was an interaction ($P= 0.050$) between the abundance of wood boring beetles and cover of brambles. The species richness of renter bees was related differently to the abundance of wood boring beetles depending on if there are brambles at the sites or not; there was a stronger increase in bee richness with increasing beetle abundance when brambles were not present (Table 8, Fig. 11). The interaction between the abundance of wood boring beetles and the presence of brambles explained 44% of the variation in the species richness of renter bees. That was higher explained variation compared to the above mentioned model where the species richness of renter bees was explained only by the abundance of wood boring beetles.

The species richness of renter bees is also positively related to the species richness of wood boring beetles. (Table 8, Fig.12). The species richness of wood boring beetles explained 23% of the variation in the species richness of renter bees. That was less explained variation compared to the two above mentioned models where the species richness of renter bees was explained by the abundance of wood boring beetles, with and without the interaction with brambles.

Table 8. The relationship between the species richness of reenter bees (solitary bees that may use abandoned insect holes as nest site) and the presence of brambles (raspberries and blackberries) and the species richness and abundance of wood boring beetles (beetles that bore holes with a diameter ≥ 3 mm in dead wood). The abundance and species richness of wood boring beetles were correlated ($r = 0.50$) and therefore treated in separate models.

Response variable	Explanatory variables	β	SE	d.f.	z	P	Pseudo- R^2
<i>Species richness of reenter bees</i>							0.40
	Intercept	-1.1	0.39	1	-2.9	< 0.01	
	Abundance of wood boring beetles	0.030	0.010	1	3.9	< 0.0001	
<i>Species richness of reenter bees</i>							0.44
	Intercept	-2.5	0.93	1	-2.6	< 0.01	
	Abundance of dead wood boring beetles	0.078	0.026	1	3.0	< 0.01	
	With brambles (vs no brambles)	1.4	1.1	1	1.2	0.21	
	Interaction bramble and abundance of dead wood boring beetles *	-0.054	0.028	1	-2.0	0.050	
<i>Abundance of reenter bees</i>							0.23
	Intercept	-1.8	0.70	1	-2.5	0.011	
	Species richness of wood boring beetles	0.25		1	0.09	2.8	

* When dropped interactions brambles x abundance wood boring beetles, the models becomes:

Intercept: $z = -2.9$, $P = < 0.01$

Abundance of reenter bees: $z = 3.9$, $P = < 0.0001$

With brambles (vs no brambles): $z = -0.72$, $P = 0.47$. Pseudo- $R^2 = 0.52 = 0.40$.

The models are generalized linear models (GLM) with poisson distribution with log link, $n = 27$. Other explanatory variables tested, but found not to be significant, are: presence of brambles (raspberries and blackberries), altitude (m), amount of forest in a diameter of 1000 meters from site (m^2), average number of standing dead trees per 20 m^2 plot, average number of logs per 20 m^2 plot, and odds measure of diversity (OD) of wood boring beetles. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in southeast part of Norway.

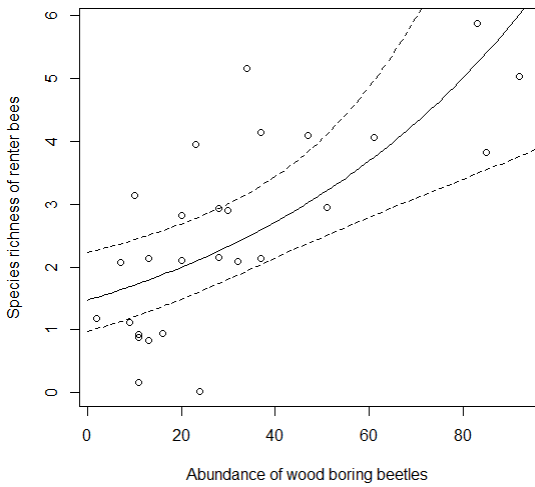


Figure 11 Species richness of renter bees (solitary bees that may use abandoned insect holes as nest site) in relation to the abundance of wood boring beetles (beetles known to bore holes greater than 3 mm in dead wood). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 8.

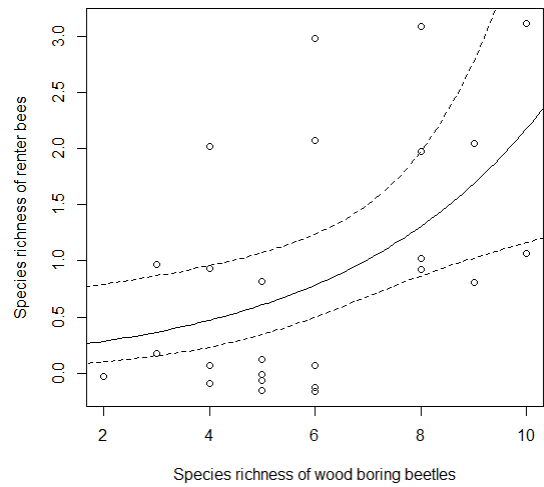


Figure 13 Species richness of renter bees (solitary bees that may use abandoned insect holes as nest site) in relation to the species richness of wood boring beetles (the beetles known to bore holes greater than 3 mm in dead wood (so-called wood boring beetles)). The observations are marked as dots included some random noise (jitter) to separate similar observations. The solid line is based on fitted values from the final generalized linear model (GLM). The dotted line is the 95% confidence interval. For Further details, see table 8.

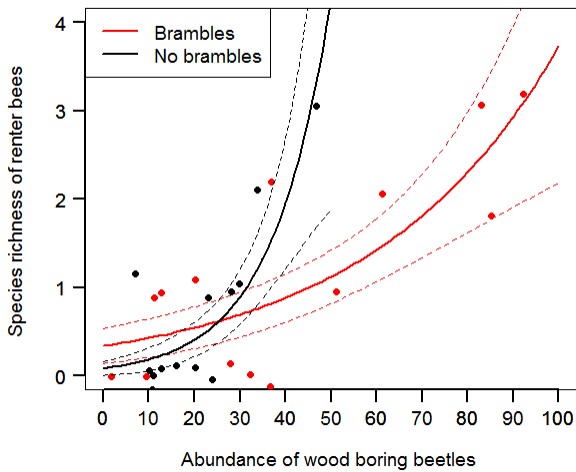


Figure 12 The species richness of renter bees (solitary bees using abandoned insect holes as nest site) were related differently to the abundance of wood boring beetles (beetles known to bore holes with a diameter greater than 3 mm in dead wood) depending on if there are brambles (red solid line) or no brambles (black solid line) at the site. The dotted lines mark the 95% confidence interval for the two models. The dots represent the observations, including some random noise (jitter) to separate similar observations. The red dots represent sites with brambles, and the black dots represent sites without brambles. The interaction between brambles and wood boring beetles got a p-value on 0.050. There are only sampled less than 50 wood boring beetles on sites without brambles, therefore the limited fitted values for the black line. For further details, see table 8.

3.2. Availability of floral resources

There was a higher abundance of cavity nesting bees in sites with plants in the *Asteraceae* family compared to sites without these plants. The presence of plants in the *Asteraceae* family explained 12 % of the variation in the abundance of cavity nesting bees. (Table 9, and Fig 14) There was also a higher abundance of renter bees in sites with plants in The *Asteraceae* family compared to sites without these plants. The presence of plants in the *Asteraceae* family explained 17 % of the variation in the abundance of cavity nesting bees. See table 9 and figure 15.

Table 9 The relation between the abundance of cavity nesting bees (solitary bees that use above ground cavities as nest sites) and floral resources represented by the presence of plants in the *Asteraceae* family. And the relationship between the abundance of renter bees (solitary bees that may use abandoned insect holes as nest site) and floral resources represented by presence of plants in the *Asteraceae* family.

Response variable	Explanatory variables	β	SE	d.f.	z	P	Pseudo- R ²
<i>Abundance of cavity nesting bees</i>							0.12
	Intercept	1.4	0.23	1	5.9	< 0.0001	
	With <i>Asteraceae</i> (vs no <i>Asteraceae</i>)	0.70	0.36	1	1.9	0.05	
<i>Abundance of renter bees</i>							0.17
	Intercept	-0.35	0.35	1	-1	0.32	
	With <i>Asteraceae</i> (vs no <i>Asteraceae</i>)	1.1	0.48	1	2.4	0.02	

The models are generalized linear models (GLM) with negative binomial distribution, and log link. n = 27. Another explanatory variabls tested, but found not to be significant, is the estimated per cent cover of species of the Fabaceae, Plantaginaceae and Lamiaceae families. The models are based on insects sampled by flight interception traps placed in power line strips at 27 different sites in southeast part of Norway.

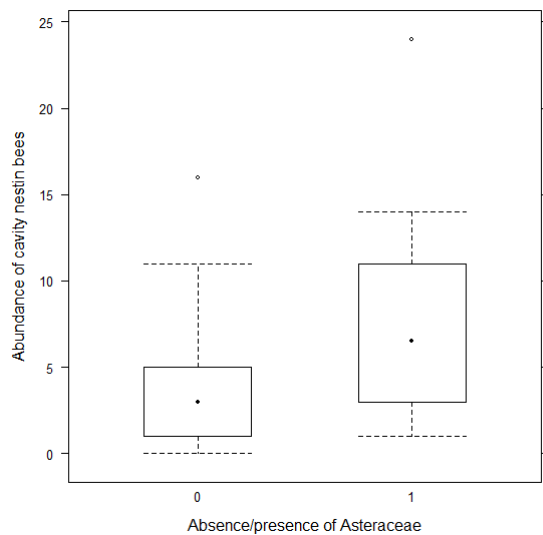


Figure 14 Boxplot of the abundance of cavity nesting bees (solitary bees nesting in above ground cavities), with (1) and without (0) plants in the Asteraceae family. When the data is ranked, the lower part of the box (the 1 quartile) represent 25 % of the data, the black dot represent the median or the 50 % of the data, and , the upper part of the box represent 75% of the data. The upper and lower whiskers represents represents respectively 90% and 10 % of the data. The open circle represents outliers. For further details see table 9

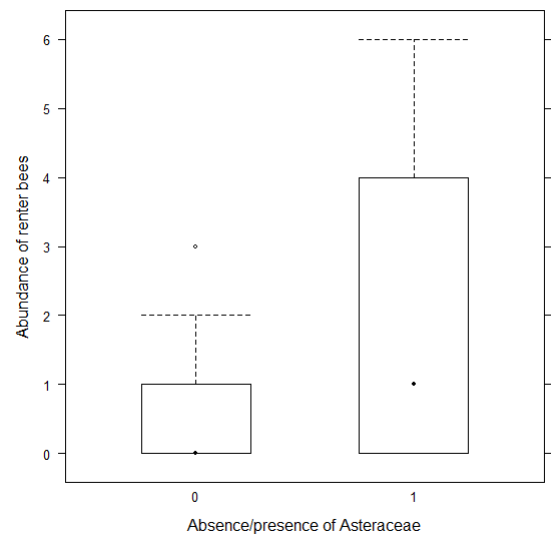


Figure 15 Boxplot of the abundance of renter bees (solitary bees that are known to use abandoned insect holes as nest sites), with (1) and without (0) plants in the Asteraceae family. When the data is ranked, the lower part of the box (the 1 quartile) represent 25 % of the data, the black dot represent the median or the 50 % of the data, and , the upper part of the box represent 75% of the data. The upper and lower whiskers represents represents respectively 90% and 10 % of the data. The open circle represents outliers. For further details see table 9

When these two models were included together with the corresponding final models, i.e., the same response variables, for nesting resource availability, no one of the floral resource variables contributed significantly to the new models.

The other explanation variables that were tested, but did not contribute significantly to the models were: altitude (m), amount of forest in a diameter of 1000 meters from site (m²), average number of standing dead trees per 20 m² plot, average number of logs per 20 m² plot, odds measure of diversity (OD) of wood boring beetles, and the per cent cover of species of the *Fabaceae*, *Plantaginaceae* and *Lamiaceae* families.

4. Discussion

Partly as expected from the hypotheses, the abundance of wood boring beetles was the most important explanatory variable to explain the abundance of cavity nesting bees. The fact that many of the cavity nesting bees may use abandoned insect holes as nest sites Westrich (1989) and that wood boring beetles create holes with a diameter similar to the trap nest diameter used by the bees (see methods) makes it reasonable to conclude that the abundance of wood boring beetles is related to the availability of nest sites for cavity nesting bees. As far as I know, there are no studies investigating the association between the abundance of cavity nesting bees and wood boring beetles. The closest study I have found is by Potts et al. (2005); they investigated how the availability of nesting resources was associated with the bee community structure. They did not find any significant associations between the abundance of old insect burrows in soil and wood, and the abundance of bees which use these old burrows as nest sites. This was a more directly count of nest sites compared to my study where the abundance of wood boring beetles was used as proxy for the availability of suitable nesting holes. In contrast to my predictions, there were no relationship between the amount of dead wood and the abundance of cavity nesting bees. This indicates that the dead wood is not a limiting resource for cavity nesting bees in this habitat. I had expected a correlation between the amount of dead wood and the abundance of wood boring beetles. Such a correlation was not to be found. The wood boring beetles are dependent on dead wood to reproduce. No association between the amount of dead wood and the abundance of wood boring beetles may indicate that dead wood is not a limiting resource for wood boring beetles in this habitat. Rather, cavity nesting bees may be limited by the availability of nest sites in dead wood, provided by the wood boring beetles. This implies that whatever influences the population of wood boring beetles also affect the abundance of cavity nesting bees as in a cascading effect (“A cascade effect is an unforeseen chain of events due to an act affecting a system.”(Xie et al. 2014, p. 338).

Even though the species richness of wood boring beetles and the presence of brambles explained much of the variation in the abundance of cavity nesting bees, they together were not as good explanatory variables as the abundance of cavity nesting beetles. The variation in abundance of cavity nesting bees explained by the species richness of wood boring beetles probably appears

because the species richness of wood boring beetles reflects the abundance of wood boring beetles. This interpretation is supported by the fact that the species richness of wood boring beetles is also correlated with the odds measurement of diversity (OD), which was not associated with the abundance of cavity nesting bees. According to this model, it is likely to find a higher abundance of cavity nesting bees when there are brambles at the site, compared to if the brambles were missing. Also a study by Potts et al. (2005) indicate that there may be an association between the availability of pithy stems (which resembles the brambles in my study) and the abundance of stem nesting bees. I had expected the brambles to contribute more to the models because the majority of the cavity nesting bees trapped in this study, approximately 75%, are grouped as obligate excavators. Additionally, I had expected the brambles to be a limited resource because their cover was relatively scarce (0-1.5%). However the fact that *Hylaeus confusus* and *Hylaeus communis*, the two most abundant species grouped as obligate excavator bees, have been found in trap nests (Gathmann et al. 1994; Steffan-Dewenter 2002) may indicate that they may use pre-existing cavities if available. Consequently, the brambles may not be that important for excavator bees. This may also elucidate why the abundance of excavator bees are best explained by the abundance of wood boring beetles.

The abundance of renter bees was best explained by interaction models where the abundance of renter bees reacts stronger on an increase in abundance of wood boring beetles when there are no brambles at the site, compared to if there were brambles at the site. This interaction may be explained by the facultative excavator bees. When there are no brambles at the sites, the facultative excavator bees have to find nest sites elsewhere, and may thereby compete with the renter bees for the nest sites in abandoned insect holes. Consequently the nest in abandoned insect holes is a more limited resource when there are no brambles at the site. One may conclude that nest sites in abandoned insect holes and brambles are important in supporting maximum abundance for both renter bees and the excavator bees. The same interaction appears when explaining the variation in species richness of renter bees. The abandoned insect holes and brambles may be important in supporting maximum species richness of both renter bees and excavator bees at a site. All this leads to the conclusion that the two functional groups, the renters and excavators, are much the same in nesting biology when there are little brambles at the site. Still the two functional groups may react differently in response to changes in amount of

brambles and abandoned beetle holes in dead wood. The relatively sparse cover of brambles (0 - 1.5%) in the sites may explain why I found little differences in limiting resources for the excavator and renter bees.

The abundance of wood boring beetles is the most important explanatory variable to explain the species richness of cavity nesting bees. Contrary to my expectations, the diversity of wood boring beetles was not related to the species richness of cavity nesting bees. This means that the species richness of cavity nesting bees is not, or only slightly associated with the species richness of wood boring beetles. The results may indicate that the bees are not that particular in their choice of cavity nesting diameter. Even though the trap- nesting bees species often differ in the main preferred nesting hole diameter, they may overlap in their range of nesting hole diameters used (Budrienè et al. 2004). Such a niche overlap may cause competition between bee species, exemplified by the findings of Strickler et al. (1996) that *Megachile relativa* nests were occupied by competing trap- nesting bee species. An increase in the number of available nesting holes may be associated with a decrease in competition and more species of cavity nesting bees can coexist. These findings indicate that there are other factors deciding the species richness of cavity nesting bees, and the abundance of wood boring beetles is only important in creating nest sites to support this species richness.

An interesting remark has to be given related to the explanatory variable altitude. The altitude did not contribute significantly to the final models, however, seen from the corelogram (Appendix 1) and the process of pre-selection of explanatory variables the altitude did show some interesting correlations. Firstly the abundance of wood boring beetles, and not species richness of wood boring beetles as one might expect, was negatively associated to the altitude. Secondly, the species richness of cavity nesting bees was also negatively associated with the altitude. According to the meta-analysis by Rahbek (1995), there are several studies demonstrating the general ecological rule saying species richness is negatively associated with increasing altitude. Even though Rahbek (1995) point out that this pattern do not always follow a straight line and may not even exist, the species richness of cavity nesting bees in my study follow the general rule fairly well. In my study, the relationship with altitude may indicate either that the altitude explains some of the variation in the abundance of wood boring beetles and

therefore indirectly explain the variation in the species richness of cavity nesting bees, or that both the abundance of wood boring beetles and the species richness of cavity nesting bees independently, in some degree, correlates with the altitude. I will not try to debate why this pattern appears in my results because the altitude represents many factors not easy to distinguish from another. Korner (2007) stress that altitude represents gradients which may be directly related to the high above sea level and other local gradients like moisture, geology, urbanization.

From this study, the abundance of cavity nesting bees is positively associated with the presence of asteraceae plants. But this association is relatively weak ($R^2 = 12\%$). As pointed out by Roulston and Goodell (2011), the majority of studies investigating resource availability for bees, conclude that floral resources are important limiting resources. However there are examples of studies where this is not the case. Grundel et al. (2010) studied the bee distribution in Northwest Indiana, USA. They did not find any relationship between the total amount of flower stems (abundance of floral resources) and the abundance of bees. Even though floral resources are essential for sustenance of viable bee populations, my study indicates that floral resources may not be the main limiting resource in power line strips.

Anthropogenic changes in land use may be associated with direct and indirect effects on local species. The change from forest to power line strips may have direct and indirect consequences for the bee species. The results from this study indicate that the power line strips directly enhance the abundance of cavity nesting bees by providing floral resources. Additionally, the power line strips indirectly affect the species richness and abundance of cavity nesting bees by providing dead wood that function as nursery for wood boring beetles, and thereby providing nest sites for renter bees. The wood boring beetles can be considered ecosystem engineers in relation to the renter bees. Ecosystem engineers are “organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats” (Jones et al. 1994, p.374). The resources provided by physical body of the organism do not count in this definition (Jones et al. 1994). The wood boring beetles may be compared to the woodpeckers, which Jones et al. (1994) pointed out as an ecosystem engineer. The woodpeckers creates holes in wood, and thereby provides nest sites for other birds and bats (Jones et al. 1994).

My study indicate that the excavator bees and renter bees may react differently in response to the availability of brambles and abandoned beetle holes in dead wood, even though they apparently are limited by the same resources. Excavator bees may persist in a habitat without abandoned beetle holes as long as there are brambles at the site. The renter bees may not. A review by Williams et al. (2010) argue for the importance of using life-history and ecological trait of bees to understand their response to environmental change. Matteson et al. (2008) divided bees into nesting guilds and observed that some guilds are more common than others in New York urban gardens. This may indicate that some functional groups of bees respond differently to urbanization. Also Williams et al. (2010) used bee nesting guilds when they conclude that renter bees react stronger to disturbance compared to the excavator bees, and that cavity nesting bees may react differently to environmental change compared to below ground nesting bees. When managing to protect the cavity nesting bees, managers have to consider, not only the availability of floral resources, but also the availability of nesting resources. The best way of protecting the cavity nesting bees in power line strips is by preserving the wood boring beetles and ensure enough brambles for the excavator bees. This study show the importance of knowing the biology and indirect species interactions of the species in concern to prevent cascading effects.

5. Acknowledgements

I would like to thank my supervisor Katrine Eldegard, my co-supervisor Markus A. K. Sydenham and project leader Stein Ragnar Moe for assisting me with great enthusiasm. I would also like to thank Jan Häusler for being a good traveling companion during field work.

6. References

- AMIET, F., MÜLLER, A. & NEUMEYER, R. (1999). Apidae. 2, Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha, Neuchâtel, Centre suisse de cartographie de la faune : Schweizerische Entomologische Gesellschaft.
- AMIET, F. (2004). Apidae. 4, Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis, Neuchâtel, Schweizerische Entomologische Gesellschaft.
- Askins, R. A., Folsom-O'Keefe, C. M. & Hardy, M. C. (2012). Effects of Vegetation, Corridor Width and Regional Land Use on Early Successional Birds on Powerline Corridors. *Plos One*, 7 (2).
- Berg, A., Ahrne, K., Ockinger, E., Svensson, R. & Soderstrom, B. (2011). Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. *Biological Conservation*, 144 (12): 2819-2831.
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schoffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., et al. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313 (5785): 351-354.
- Bjørndal, I. & Bjørkelo, K. (2006). *AR5 klassifikasjonssystem: klassifikasjon av arealressurser*, vol. 01/2006. Ås: Norsk institutt for skog og landskap. 25 pp.
- Budrienė, A., Budrys, E. & Nevronytė, Z. (2004). Solitary Hymenoptera Aculeata Inhabiting Trap-Nests in Lithuania: Nesting Cavity Choice and Niche Overlap. *Latvijas Entomologs*, (41): 19-31.
- Cadotte, M. W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48 (5): 1079-1087.
- Crawley, M. J. (2013). *The R book*. Chichester, West Sussex, U.K.: Wiley. 1 online resource (1 b.) 1076 pp.
- Daily, G. C. (1997). *Nature's services: societal dependence on natural ecosystems*. Washington, DC: Island Press. 392 pp.
- Danks, H. V. (1971). NEST MORTALITY FACTORS IN STEM-NESTING ACULEATE HYMENOPTERA. *Journal of Animal Ecology*, 40 (1): 79-82.
- Diaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16 (11): 646-655.

- Ehnström, B. & Axelsson, R. (2002). *Insektsnag i bark och ved*. Uppsala: Artdatabanken, SLU. 512 pp.
- Fauna entomologica Scandinavica*. Klampenborg: Scandinavian Science Press.
- Freude, H., Harde, K. W. & Lohse, G. A. (1964). *Die Käfer Mitteleuropas*. Krefeld: Goecke & Evers. b. : ill. pp.
- Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. (2006). Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *Plos Biology*, 4 (1): 129-135.
- Gathmann, A., Greiler, H. J. & Tschardtke, T. (1994). TRAP-NESTING BEES AND WASPS COLONIZING SET-ASIDE FIELDS - SUCCESSION AND BODY-SIZE, MANAGEMENT BY CUTTING AND SOWING. *Oecologia*, 98 (1): 8-14.
- Gathmann, A. & Tschardtke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71 (5): 757-764.
- Greenleaf, S. S. & Kremen, C. (2006). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences of the United States of America*, 103 (37): 13890-13895.
- Grundel, R., Jan, R. P., Frohnapple, K. J., Glowacki, G. A., Scott, P. E. & Pavlovic, N. B. (2010). Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*, 20 (6): 1678-1692.
- Hoehn, P., Tschardtke, T., Tylianakis, J. M. & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B-Biological Sciences*, 275 (1648): 2283-2291.
- Hoiss, B., Krauss, J., Potts, S. G., Roberts, S. & Steffan-Dewenter, I. (2012). Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B-Biological Sciences*, 279 (1746): 4447-4456.
- Jones, C. G., Lawton, J. H. & Shachak, M. (1994). ORGANISMS AS ECOSYSTEM ENGINEERS. *Oikos*, 69 (3): 373-386.
- Korner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, 22 (11): 569-574.
- Kvalseth, T. O. (1991). NOTE ON BIOLOGICAL DIVERSITY, EVENNESS, AND HOMOGENEITY MEASURES. *Oikos*, 62 (1): 123-127.
- Landin, B.-O. (1957). *Svensk insektfauna. 9: skalbaggar - coleoptera : bladhorningar -*

- lamellicornia* : fam. scarabaeidae. Stockholm: Entomologiska föreningen i Stockholm. 155 pp.
- Matteson, K. C., Ascher, J. S. & Langellotto, G. A. (2008). Bee richness and abundance in New York city urban gardens. *Annals of the Entomological Society of America*, 101 (1): 140-150.
- Michener, C. D. (2007). *The bees of the world*. Baltimore: Johns Hopkins University Press. 1 online resource, 953 pp.
- Nationalnyckeln till Sveriges flora och fauna*. Uppsala: ArtDatabanken, Sveriges lantbruksuniversitet, 2005- .
- Palm, T. (1959). *Die Holz- und Rinden-Käfer der Syd- und Mittelschwedischen Laubbäume*, vol. 16. Lund: Sällskapet. 374 pp.
- Petchey, O. L. & Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, 9 (6): 741-758.
- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G. & Willmer, P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30 (1): 78-85.
- R Core Team. (2012). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0. URL: <http://www.R-project.org>.
- Rahbek, C. (1995). THE ELEVATIONAL GRADIENT OF SPECIES RICHNESS - A UNIFORM PATTERN. *Ecography*, 18 (2): 200-205.
- Rennerfelt, E. (1951). *Die Holz- und Rinden-Käfer der nordschwedischen Laubbäume*, vol. 40:2. Stockholm: Institutet. 242 pp.
- Romey, W. L., Ascher, J. S., Powell, D. A. & Yanek, M. (2007). Impacts of logging on midsummer diversity of native bees (Apoidea) in a northern hardwood forest. *Journal of the Kansas Entomological Society*, 80 (4): 327-338.
- Roulston, T. H. & Goodell, K. (2011). The Role of Resources and Risks in Regulating Wild Bee Populations. In Berenbaum, M. R., Carde, R. T. & Robinson, G. E. (eds) *Annual Review of Entomology*, vol. 56 *Annual Review of Entomology*, Vol 56, pp. 293-312.
- Ruggiero M. (project leader). (2009). Ascher J. et al. (2014). ITIS Bees: World Bee Checklist (version Sep 2009). In: Species 2000 & ITIS Catalogue of Life, 2014 Annual Checklist (Roskov Y., Kunze T., Orrell T., Abucay L., Paglinawan L., Culham A., Bailly N., Kirk P., Bourgoin T., Baillargeon G., Decock W., De Wever A., Didžiulis V., eds). Digital resource at www.catalogueoflife.org/annual-checklist/2014. Species 2000: Naturalis,

Leiden, the Netherlands.

- Russell, K. N., Ikerd, H. & Droege, S. (2005). The potential conservation value of unmowed powerline strips for native bees. *Biological Conservation*, 124 (1): 133-148.
- Silfverberg, H. (2004). *Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae*, vol. Vol. 9:1. Helsingfors: Zoologiska museet. 111 pp.
- Skogoglandskap. (2014). Kilden- til arealinformasjon. Available at: <http://kilden.skogoglandskap.no> (accessed: 02.05.2014).
- Steffan-Dewenter, I. (2002). Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology*, 27 (5): 631-637.
- Steffan-Dewenter, I. & Schiele, S. (2008). Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology*, 89 (5): 1375-1387.
- Strickler, K., Scott, V. L. & Fischer, R. L. (1996). Comparative nesting ecology of two sympatric leafcutting bees that differ in body size (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, 69 (1): 26-44.
- The Norwegian Biodiversity Information Centre. Artsnavnebase. Available at: <http://www2.artsdatabanken.no/artsnavn> (accessed: January 2014).
- Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S. Fourth Edition*. New York: Springer.
- Watanabe, M. E. (1994). POLLINATION WORRIES RISE AS HONEY-BEES DECLINE. *Science*, 265 (5176): 1170-1170.
- Westrich, P. (1989). Die Wildbienen Baden-Württembergs, Stuttgart, E. Ulmer.
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In Matheson, A., Williams, I. H., Buchmann, S. L., O'Toole, C. & Westrich, P. (eds) vol. no. 18 *The Conservation of bees*, pp. VIII, 254. London: Academic Press. pp. 1-16.
- Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L. & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143 (10): 2280-2291.
- Winfree, R., Williams, N. M., Dushoff, J. & Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10 (11): 1105-1113.
- Wright, K. (2013). Corrgram: Plot a correlogram. R package version 1.5. URL: <http://CRAN.R-project.org/package=corrgram> }.

Xie, W., Li, N., Li, C. H., Wu, J. D., Hu, A. J. & Hao, X. L. (2014). Quantifying cascading effects triggered by disrupted transportation due to the Great 2008 Chinese Ice Storm: implications for disaster risk management. *Natural Hazards*, 70 (1): 337-352.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1 (1): 3-14.



Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no